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REBECCA F. SURDICK

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Abstract

The ten Nearctic genera of the subfamily Chloroperlinae (Chloroperlidae; Plecoptera; Insecta) are examined and redescribed, along with the original description of *Plumiperla* new genus. Three tribes are designated for the Holarctic fauna and the phylogeny of the subfamily is discussed. Biogeographic study of Nearctic genera indicates the effects of Pleistocene glaciations on distributions. Generic keys to males, females and larvae are presented.

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Introduction

The subfamilies Chloroperlinae and Paraperlinae comprise the Chloroperlidae, one of nine families of Nearctic Plecoptera. Holarctic in distribution, fifteen genera are recognized within the subfamily Chloroperlinae. Ten genera and 63 species constitute the North American fauna.

Based on the genus *Chloroperla* Newman 1836, the subfamily Chloroperlinae was erected under the family Perlidae by Okamoto in 1912 and also included species presently recognized as *Isoperla* (Isoperlinae; Perlodidae). The first Nearctic species, *Alloperla imbecilla*, was described in 1823 by Say as *Sialis imbecilla* and shared the generic assignment with *Pteronarcys dorsata* (Say), *Isoperla bilineata* (Say) and *Paragnetina immarginata* (Say). Hagen (1861) included chloroperlids in the broad genus *Perla*.

With the establishment of *Chloroperla* Newman 1836, based on the European *Chloroperla tripunctata* (= *Phryganea tripunctata* Scopoli 1763), chloroperlids were distinguished from *Perla* by parallel costal and subcostal veins and reduction in number of crossveins in the wings. In 1906, Banks synonymized *Chloroperla* with *Isopteryx* Pictet 1841 and included in the genus mostly European representatives lacking a folded anal area in the hindwing. He defined *Alloperla* and *Isoperla* based on wing venation and assigned Nearctic chloroperlids, including *Haploperla brevis* (Banks 1895) in 1907, to *Alloperla*.

Frison (1942) established Isoperlidae and Chloroperlidae as distinct families. Ricker (1943, 1950, 1952) divided the latter into subfamilies Chloroperlinae and Paraperlinae, and proposed four subgenera of *Alloperla: Alloperla* (sensu stricto), *Sweltsa*, *Suwallia*, *Neaviperla* and *Triznaka;* and one subgenus of *Chloroperla: Rasvena*. In 1966, Illies elevated the subgenera to generic status.

The research as here reported has attempted to appraise the status of subfamily Chloroperlinae in North America. Genera have been more clearly defined, phylogenetic relationships have been hypothesized and evidence of biogeographic history has been assessed.

Materials and Methods

Collecting, rearing and field observation accompanied usual laboratory methods. More than 10,000 specimens of Nearctic Chloroperlinae, as well as examples of Palearctic species, were examined. Inspection of terminalia and other body structures was facilitated by heating the section in 10% potassium hydroxide and water to remove nonsclerous tissue. Adult and larval mouthparts, and other minute structures were mounted on microscope slides.

When possible, ova were photographed with a scanning electron microscope. Best results were obtained by using very ripe ova that had been washed in distilled water and mounted on stubs with double-faced tape.

Morphology

The identity of the family Chloroperlidae as part of the group Systellognatha and superfamily Subulipalpia has been outlined by Zwick (1973, 1974). Characters shared with other systellognaths include nonorthopteroid adult mandibles, well-developed epiproct set in a cleft tenth tergite, well-developed longitudinal muscles and postnotum firmly connected with pleura by a postalar bridge. The Subulipalpia exhibit specialized larval mouthparts, micropyles on the ovum opposite the collar, and shortened first two tarsal segments. Chloroperlidae are characterized by reduced wing venation, seven abdominal ganglia, three ocelli and unmodified paraprocts. Penultimate segments of the maxillary and mandibular palpi are swollen, and each minute terminal segment is attached asymmetrically to the penultimate one.

The two subfamilies are distinguished on the basis of several characters. First, the anal fan of the hindwing of Chloroperlinae has been reduced to a maximum of four veins, in contrast to a maximum of seven in Paraperlinae. Second, tearing mandibles present in adult Chloroperlinae are reduced in adult Paraperlinae. Third, in Chloroperlinae, the distal extension of the male epiproct is recurved anteriorly, and the basal bar is flattened, fused to the anterior of segment ten. In Paraperlinae, the posterior extension of the epiproct is retained, and the basal bar is deeply inset, projecting into segment nine (Zwick 1973).

Characters employed in distinguishing genera, assembling species groups and estimating relationships principally involve differences in anatomy and setation. Adult coloration, although previously a major criterion of generic distinction, has been de-emphasized in this study

because of its variability, usual absence in teneral specimens, and tendency to fade in preservation.

The shapes of adults and larvae are useful field identification marks and reflect the burrowing ability of the larvae (personal observation; J. Stanford, personal communication; Hynes 1976). The generally uniform tan, gill-less larvae are small (to 15 mm), elongate stoneflies with wingpads laterally rounded, close to the body. The tube shape and the amount of lateral extension or flattening of the pronotum appear to vary with the burrowing habits and habitat of the species. Although specific taxonomic differences are slight, genera are distinguished by subtleties in head and pronotum shapes, setation, mouthparts and color pattern. Body setation varies in length and thickness of clothing hairs, scattered "guard" hairs, fine fringe hairs and regular, bristly fringes of segment margins.

The delicate (5–15 mm long) adults vary in color from light yellow to lime green to tan and many bear distinctive dark markings (Figs. 1, 2, 63). Field marks distinguishing genera and often species include head and pronotum shapes, wing reduction and differences in pigmentation of the meso- and metascutellar "U" area. Conspicuous body setation is sparse and variously darkened. Reduction in wing size and venation is probably, in part, an aerodynamic or physical response accompanying reduced body size (Ricker 1943). Restrictions placed on the development of the immature stages by the environment can also be involved. Physiological responses to temperature and photoperiod, adaptations of larvae to stream currents and burrowing, adjustment of the life cycle and genetics are important in the shaping of larval wingpads and the development of adult wings in late instars (G. F. Edmunds, Jr., personal communication; Hinton 1948; Nebeker and Gaufin 1967; Sweeney and Vannote 1978). In cases of brachyptery and pterygomorphism, lack of flight ability from severe wing reduction can inhibit dispersal, and be advantageous in restricting emigration from an isolated or environmentally specialized population in a permanent habitat (Hynes 1972, 1976; Brinck 1949; Ross and Ricker 1971). Brachyptery is common in some *Sweltsa* populations, particularly those in high altitude springs and lakes.

Characters of the adult abdomen are used both to separate species and genera for identification and to group them by similarity to indicate relationship. Well-developed adult features in pharate speci-

mens permit accurate association of adult with larva. Detailed studies of internal and external anatomy of representative Chloroperlinae were reported by Brinck (1956) and Zwick (1967, 1971, 1972, 1973, 1977).

External male terminalia (Fig. 13) consist of a modified tenth tergum bearing the genital apparatus. The tenth tergum is cleft in all Chloroperlinae, and the hemiterga may be extended to form digitate processes. The medially located and specifically unique epiproct is composed of a basal anchor, set in the anterior of segment 10, connected via a basal bar to the frequently hinged epiproct tip, posteriorly adjoining the anal lobe. Additional support for the often erectable epiproct tip is provided by paragenital plates and lightly sclerotized, transverse bands at the bases of the hemiterga. Occasionally, the cushioning membranous area, which surrounds the distal end of the basal bar and enfolds the unerected epiproct tip, is enlarged to form a cowl. The terminalia are essentially bilaterally symmetrical and paraprocts are unmodified. Cerci are many-segmented and unmodified, except in *Neaviperla* (Fig. 100). Zwick (1973) considered the small knobs on the base of the epiproct in *Sweltsa* to be remnants of lateral stylets (Fig. 80) and discussed the muscles involved in the erection of the epiproct.

Transverse ridges may be present on tergum 8 or 9 (Figs. 75, 80) and a hammer is present in *Triznaka* and male *Rasvena* on abdominal sternum 7 (Figs. 115, 150). Brushes of multiple bristles may be present on lateral edges of terminal segments (Fig. 80). Sternum 9 is produced posteriorly and accommodates the contracted aedeagus. The aedeagus is specialized, but seldom variable within a genus. Brinck (1956) and Zwick (1967, 1973) refer to the function of the accessory glands.

Female genitalia include the variously shaped subgenital plate, extending posteriorly from the middle or posterior of sternum 8, and covering the genital opening. Subgenital plate and sterna 8 and 9 may bear distinctive setal patterns, a hammer, or lateral brushes. The vagina may be membranous or lightly sclerotized and spinulated. Internal organs have been described by Brinck (1956) and Zwick (1967, 1973). Cerci and paraprocts are unmodified, except in *Neaviperla* (Fig. 106).

Observations were made on the mating of *Sweltsa coloradensis*

(Banks) from South Willow Canyon, Tooele Co., Utah. Specimens were examined in a small petri dish with a stereomicroscope at 20× and 40× magnifications.

The male mounted the female, head even with female's pronotum, and curled its abdomen in an S-shape around to the underside of the female's abdomen. Thus, the male's abdominal terga abutted the female's abdominal sterna. The epiproct was hooked beneath the subgenital plate of the female and quickly slid from side to side under the plate for about 5 minutes. Abruptly, the membranous, blunt-ended aedeagus was everted and a large drop of seminal fluid was deposited in the hollow of the female's sternum 9, against the down-lifted subgenital plate. The aedeagus was then retracted without entering the genital opening, and the male proceeded to gently pat the subgenital plate with terga 9 and 10. This appeared to stimulate the female to take in the fluid via the genital pore. When the fluid had disappeared, the pair uncoupled. The encounter lasted about 10 minutes.

Mating behavior of *Xanthoperla apicalis* (Newman) was described by Brinck (1956). In those stoneflies, the tubelike aedeagus of the male was inserted in the female genital cavity. The aedeagus bears various spinules, sclerotized bars and a chitinous penis head to support the erigated organ and hold it in the similarly spinulated vagina.

The above descriptions of copulation illustrate two general examples found within the subfamily Chloroperlinae. In each case, internal and external modifications of the genital apparatus correlate with function and behavior. The membranous aedeagus, and membranous, unthickened vagina of *Sweltsa coloradensis* require no further modification since the structures do not come in contact. The blunt-ended aedeagus covers the depressed ninth sternum. The tubular, spinulated, well-supported aedeagus and the thickened, spinulated vagina of *Chloroperla* (sensu lato), however, are morphologically prepared for encounter.

Mandibles of adult Chloroperlidae may be developed and sclerotized or much reduced (Figs. 16–18). Functional, developed mandibles probably correlate with the necessity of adult feeding and the maturation of the ova. Females of most Chloroperlinae do not contain mature ova upon adult emergence. Eggs mature later, generally several at a time, and are not always carried externally in a mass prior to

release, as in some Plecoptera. In some cases, however, well-developed ova were found in mature larvae of *Suwallia* sp. from Alaska and Wyoming.

Most chloroperline ova are tan or golden brown and ovoid. Taxonomic characters include shape, punctation and presence or absence of a collar. As with adults and larvae, specific differences are seldom great and generic characters are few.

Key to Genera of Nearctic Chloroperlinae

ADULT MALES

1. Epiproct tip variously sculptured, hinged (Figs. 64–67, 75, 79–80, 82–84, 88); basal bar of epiproct thin, curved, attached to three- to five-times wider, cupped anchor (Figs. 67, 79, 88); brush of closely set and multiple hairs on posterolateral margins of terminalia (Figs. 65, 80) 2

 Epiproct tip tablike or buttonlike, not hinged (Figs. 91–93, 100, 102, 103, 109–111, 124–126, 137–139, 147–149, 155–157); basal bar twice as long as, or as long as, thick, merged with equally wide anchor (Figs. 93, 103, 111, 126, 139, 149, 157); evenly spaced hairs on posterolateral margins of terminalia (Fig. 92) 4

2. Epiproct tip uninflated, or flat and curled (Figs. 82–84, 88); basal anchor sequentially double (Figs. 82, 88) *Bisancora*

 Epiproct tip inflated, sculptured (Figs. 67, 79); basal anchor single (Figs. 67, 79) 3

3. Integument generally more heavily chitinized, darker-pigmented with various pronounced brown or black markings on head or pronotum (Fig. 4), dark abdominal stripe; sutures darkly marked; transverse ridge present on tergum 9 (except in *S. occidens*) (Figs. 75, 80); epiproct tip usually extending anteriorly beyond tergum 10 (Figs. 75, 80) *Sweltsa*

 Integument generally more lightly chitinized, paler-pigmented with only pale dusky or no markings on pronotum, abdomen (Fig. 3); sutures not darkly marked; transverse ridge absent on tergum 9 (Figs. 64, 65); epiproct tip usually not extending anteriorly beyond tergum 10 (Figs. 64, 65) *Alloperla*

4. Epiproct tip buttonlike (Figs. 93, 103); hemiterga of segment 10 extended to form digitate processes (Figs. 91, 92, 100, 102) 5
 Epiproct tip tablike (Figs. 111, 126, 139, 149, 157); hemiterga not extended 6
5. Tergum 9 with anteriorly projecting process (Figs. 99, 101); basal segments of cerci elongated, convexly curved (Figs. 100, 102) *Neaviperla*
 Tergum 9 not modified (Figs. 91, 92); cerci not modified (Figs. 91, 92) *Suwallia*
6. Aedeagus lacking distinct skeletal support rods (Figs. 112, 127); anal vein of forewing branched (Figs. 21, 23) 7
 Aedeagus with pair of distinct, curved skeletal support rods (Figs. 140–143, 151, 158); anal vein of forewing branched or unbranched (Figs. 20, 22, 24) 8
7. Aedeagus terminating in pair of thin, feathery processes (Figs. 127–129); hammer absent *Plumiperla*
 Aedeagus lacking thin, feathery processes (Figs. 112–114); hammer present (Fig. 115) *Triznaka*
8. Anal area of hindwing greatly reduced, without fold (Fig. 20); Rs of hindwing usually not branched beyond cord (Fig. 20) *Haploperla*
 Anal area of hindwing entire or slightly reduced, with fold (Figs. 22, 24); Rs of hindwing branched beyond cord (Figs. 22, 24) 9
9. Epiproct tip pointed, as long as wide, protruding from prominent, hairy anal lobe (Figs. 147–149) *Rasvena*
 Epiproct tip rounded, 3 times longer than wide, arching above less conspicuous anal lobe (Figs. 155–157) *Chloroperla* (s.l.) *ovibovis*

ADULT FEMALES

1. Brush of closely set and multiple hairs on posterolateral margins of terminalia (Figs. 71, 73) 2
 Evenly spaced hairs on posterolateral margins of terminalia (Fig. 97) 4
2. Scalloped subgenital plate with long hairs only on posterior margins of lateral scallops (Figs. 89, 90); median ridge of

mesobasisternal Y-ridge extended nearly to mesosternacosta (Fig. 15) *Bisancora*

Variously shaped or scalloped subgenital plate without long hairs only on posterolateral angles (Figs. 70–73); median ridge of mesobasisternum not extended beyond split of Y-ridge (Fig. 14) 3

3. Integument generally more heavily chitinized, darker-pigmented with various pronounced brown or black markings on head or pronotum (Fig. 4), dark abdominal stripe; sutures darkly marked; subgenital plate obviously originates near anterior of sternum 8 (Figs. 72, 73) *Sweltsa*

Integument generally more lightly chitinized, paler-pigmented with only pale dusky or no markings on head, pronotum (Fig. 3), abdomen; sutures not darkly marked; subgenital plate appears to arise near posterior margin of sternum 8 (Figs. 70, 71) *Alloperla*

4. Vagina membranous; mandibles weakly developed, little sclerotized (Figs. 17, 18) 5

Vagina thickened or spinulated; mandibles developed, sclerotized (Fig. 16) 6

5. Basal segments of cerci elongated (Fig. 106); dark recurrent scutoscutellar suture bisected by dark line (Fig. 7)..... *Neaviperla*

Cerci not modified; dark recurrent scutoscutellar suture not bisected by dark line (Fig. 6) *Suwallia*

6. Anal area of hindwing greatly reduced, without fold (Fig. 20); Rs of hindwing usually not branched beyond cord (Fig. 20) *Haploperla*

Anal area of hindwing entire or slightly reduced, with fold (Figs. 21, 22, 23, 24); Rs of hindwing branched beyond cord (Figs. 21, 22, 23, 24) 7

7. Subgenital plate ⅓ width of sternum, appearing as small, posterior extension of sternum 8 (Figs. 152, 153) *Rasvena*

Flaplike subgenital plate ⅔ width of sternum, arising from indentation anterior to posterior margin of sternum 8 (Figs. 116, 117, 130, 131, 159, 160) 8

8. Anal vein of forewing unbranched (Fig. 24)..... *Chloroperla* (s.l.) *ovibovis*

Anal vein of forewing branched 9

9. Habitus delicately sclerotized; not darkly pigmented or patterned (Fig. 9) *Plumiperla*
Habitus heavily sclerotized; darkly pigmented, distinctly patterned (Fig. 8) *Triznaka*

LATE INSTAR LARVAE

1. Maxillae terminating in large single tooth and variously sized comb of equal length, evenly spaced teeth (Figs. 35, 36); fringe hairs of pronotum sparsely clustered or single and on corners only (Fig. 26) *Alloperla*
Maxillae terminating in single large and single small tooth (Fig. 34); fringe hairs of pronotum at least numerous on anterior, posterior margins (Figs. 27–33) 2
2. Distal ⅔ cercal segments posteriorly fringed with a whorl of several fine hairs, up to twice segment length (Fig. 47) and inner margins of wingpads oblique *Sweltsa*
Distal ⅔ cercal segments posteriorly fringed with only 2 to 4 long, fine hairs, generally directed only dorsally and ventrally and shorter to just longer than segment (Figs. 48–51, 53); or cercal segments fringed with whorl of long hairs (Fig. 52) and inner margins of wingpads nearly parallel 3
3. Pronotal fringe hairs (Figs. 32, 33), other long body hairs nearly as long as abdominal segment, half pronotum width; inner margins of wingpads nearly parallel (Figs. 146, 154) .. 4
Pronotal fringe hairs (Figs. 28–31), other long body hairs ⅔ length of abdominal segment, ⅓ pronotum width; inner margins of wingpads widely or only slightly oblique (Figs. 98, 122, 123) 5
4. Fine clothing hairs minimal; pronotal fringe sparse or short laterally, anteromedially (Fig. 32); abdomen concolorous (Fig. 146) *Haploperla*
Fine clothing hairs thick; pronotal fringe thick, nearly complete except laterally (Fig. 33); abdomen dusky striped (Fig. 154) *Rasvena*
5. Pronotal fringe sparse or absent laterally, not uniform (Figs. 28, 29); short fringe on posterior margins of abdominal terga not regular or uniform; long fine hairs of cerci shorter than segment (Figs. 48, 49); abdomen concolorous, or with pale longitudinal median stripe, but not checkered (Fig. 98) *Suwallia* and *Neaviperla*

Pronotal fringe thick, regular, uniform, nearly complete, or sparse only laterally (Figs. 30, 31); short fringe on posterior margins of abdominal terga uniform, thick; long fine hairs of cerci longer than segment (Figs. 50, 51); abdomen nearly concolorous or with pale checkered patterns (Figs. 122, 123) 6

6. Abdomen distinctly patterned (Figs. 122, 123); pronotal fringe regular, nearly complete (Fig. 30); inner margins of wingpads widely oblique *Triznaka*

Abdomen generally concolorous (Fig. 136); pronotal fringe sparse laterally (Fig. 31); inner margins of wingpads slightly oblique *Plumiperla*

Bisancora, *Chloroperla* (s.l.) *ovibovis* unknown

Alloperlini New Tribe

Epiproct tip hinged; sclerotized paragenital plates and elongated basal bar attached to prominent basal anchor, functioning to support and elevate epiproct tip; anal lobe small. Hemiterga of segment 10 unmodified. Aedeagus expanded apically, not spinulated. Vagina membranous. Adult mandibles normally dentate.

Alloperlini includes the genera *Alloperla* Banks, *Sweltsa* Ricker and *Bisancora* Surdick and is represented in the eastern and western Nearctic and the eastern Palearctic including Japan and Korea.

Alloperla Banks

Alloperla Banks, 1906: 175. Type species: *Alloperla imbecilla* Say.

DESCRIPTION

Adult

Body length 5 to 13 mm. Lime green, yellow or light tan, generally delicately sclerotized; lacking dark markings except for dark ocellar rings; tarsal apices, basal and terminal antennal segments, thoracic sutures, pronotal stripe, margin or reticulations, abdominal stripe dusky in some species. Head with compound eyes set near posterior corners and occiput abruptly tapered posteriorly, or with compound eyes set slightly forward and occiput elongated; mandibles with 4 or 5 sclerotized teeth. Pronotum rectangular or nearly square; corners rounded; width less than or equaling head width; nearly smooth to delicately rugose. Wings hyaline with forewing A2 branched; folded hindwing anal area with 3 veins; Rs of fore- and hindwing branched beyond cord; macropterous. Mesosternal Y-ridge unmodified. Terminal abdominal segments with lateral brushes of multiple hairs;

hammer absent; up to 7 abdominal segments with pleural folds. Cerci unmodified; 8–18 segments. (Figs. 3, 14, 16; *see also* 19)

Male

Tergum 9 frequently slightly indented medially on posterior margin, otherwise unmodified; hemiterga 10 unmodified; transverse bands sclerotized, thick. Epiproct erectile, moderately sclerotized, nearly hidden when relaxed in membranous groove between hemiterga; anal lobe inconspicuous. Epiproct tip hinged, recurved anteriorly, generally small, not extending beyond tergum 10; variously inflated, sculptured, setose, sclerotized; occasionally cushioned by enlarged cowl formed from membranous area surrounding distal end of basal bar. Basal bar concave ventrally, as thin as or thinner than and not fused with paragenital plates. Basal anchor set on anterior margin tergum 10, extending almost beneath posterior tergum 9 when relaxed; ½ as long, to as long as, wide; ½ width tergum. Membranous aedeagus tubular basally, extending to slightly swollen or enlarged, dish-faced apex with 2 small posterior, 2 large anterior, lobes. (Figs. 64–69)

Female

Sternite 9 slightly concave, sparsely setose. Subgenital plate variously shaped and setose, usually a subtriangular or round margined flap covering genital pore and overlapping anterior tergum 9 by various lengths; generally appearing as posterior extension of sternum 8, although sternum 8 may be medially flattened, with slight lateral indentations at termination of posterior segmental fringe that marks plate intersection with sternum margin; plate base ½ to ¾ segment width, projecting flap may be ¼ to ½ segment width; projecting flap in profile thin, concave, convex or inflated, often terminating in long setae. Vagina membranous. (Figs. 70, 71)

Larva

To 13 mm. Light yellow-tan to tan, usually concolorous. Head with compound eyes set near posterior corners and occiput abruptly tapered posteriorly, or with compound eyes set slightly forward and occiput elongated. Maxilla terminating in single tooth and comb of 2 to 10 regularly spaced, even-length teeth; dorsal aspect of paraglossa usually with thick row of staggered bristles on inner margin, scattered

bristles on remainder of surface. Pronotum rectangular or nearly square, corners rounded; width less than or equaling head width; fringe of single or clustered long hairs restricted to corners. Wingpads convex on outer margins, nearly parallel to oblique on inner margins. Mesosternal Y-ridge unmodified. More circularly tubular abdomen, narrower pronotum, wingpads yielding more elongate habitus than other genera. Clothing hairs fine, pale, sparse; bristle fringes and scattered long hairs of posterior abdominal tergal margins sparse medially. Cerci featherlike; each segment on distal cerci with one to a few dorsal and ventral fine hairs extending posteriorly from posterior margin and as long as, to longer than, segment; also with delicate hairs in dorsal and ventral longitudinal rows along segments; 10–16 segments. (Figs. 26, 35, 36, 39, 46, 74)

Ovum

Ovoid to skewed ovoid, circular cross section; golden tan to light brown; chorion finely to grossly punctate. Collar, when present, flanged, incised; with short or no stalk; often surrounded by smooth halo basally. (Figs. 54, 55)

DISTRIBUTION AND NEARCTIC SPECIES LIST: *Alloperla* Banks

Eastern, western Nearctic; 20 eastern Palearctic species, including 7 in Japan and 2 in Korea.

aracoma Harper and Kirchner 1978, West Virginia.
atlantica Baumann 1974, eastern Nearctic.
banksi Frison 1942, Nova Scotia, New York west to Michigan.
biserrata Nelson and Kondratieff 1980, western Virginia.
caudata Frison 1934, eastern Nearctic west to Oklahoma, Arkansas, Illinois.
chandleri Jewett 1954, California.
chloris Frison 1934, eastern Nearctic.
concolor Ricker 1935b, northeastern Nearctic.
delicata Frison 1935a, Oregon, California.
fraterna Frison 1935a, Pacific Northwest, California.
furcula Surdick 1981, South Carolina.
hamata Surdick 1981, Alabama.
idei (Ricker) 1935a, eastern Nearctic.

imbecilla (Say) 1823, Ohio River drainage.
leonarda Ricker 1952, Maine west to Michigan, Minnesota.
medveda Ricker 1952, northern Rocky Mts.
nanina Banks 1911, southern Appalachian Mts.
natchez Surdick and Stark 1980, Mississippi.
neglecta Frison 1935a, southern Appalachian Mts.
pilosa Needham and Claassen 1925, Colorado.
roberti Surdick 1981, Illinois.
serrata Needham and Claassen 1925, Alaska, northern Rocky Mts.
severa (Hagen) 1861, Alaska, northern, central Rocky Mts., Washington, Oregon.
usa Ricker 1952, eastern Nearctic.
voinae Ricker 1948, northeastern Nearctic.
vostoki Ricker 1948, northeastern Nearctic.

MATERIAL EXAMINED

Alloperla aracoma—WEST VIRGINIA: Logan Co.

A. atlantica—MAINE: Hancock, Washington Cos. MARYLAND: Baltimore, Frederick Cos. MICHIGAN: Ontonagon Co. MINNESOTA: Cook, St. Louis Cos. NEW BRUNSWICK: Chatham; Chester Basin. NEW HAMPSHIRE: Jefferson, Merrimack Cos. OHIO: Adams Co. PENNSYLVANIA: Chester Co. QUEBEC: Gatineau Pk.; Godbout; Great Whale R.; Hippolyte; Pk. Mt. Tremblant; R. Nabisipi; St. Patrice; South Boulton. SOUTH CAROLINA: Oconee, Pickens Cos. TENNESSEE: Monroe Co.; Great Smoky Mts. Natl. Pk. VIRGINIA: Craig, Giles, Montgomery, Rappahannock Cos.

A. banksi—MICHIGAN: Crawford, Lake, Ogemaw Cos. NEW YORK: Montgomery, Otsego, Tompkins Cos. NOVA SCOTIA: Truro. ONTARIO: Durham, Peel Cos. QUEBEC: St. Vallier.

A. biserrata—VIRGINIA: Augusta, Bath, Montgomery, Rockingham Cos. WEST VIRGINIA: Pendleton, Pocahontas Cos.

A. caudata—ARKANSAS: Carroll, Washington Cos.; Mt. Pine. GEORGIA: Gilmer, Fannin, Towns Cos. ILLINOIS: Hutchins Crk.; La Rue. MAINE: Washington Co. MISSOURI: Roaring R. St. Pk. NEWFOUNDLAND: Burgeo; Stephenville. NEW HAMPSHIRE: Coos, Grafton Cos. NEW YORK: Adirondack Pk. NORTH CAROLINA: Buncombe Co.; Great Smoky Mts. Natl. Pk. NOVA SCOTIA: Baddeck; Truro. OHIO: Geauga Co. OKLAHOMA: Adair Co. ON-

TARIO: Peel Co.; Kilgaire. QUEBEC: Isle d'Orléans; Knowlton. TENNESSEE: Monroe Co. VERMONT: Orange Co. VIRGINIA: Augusta, Bath, Page, Rockingham, Shenandoah Cos.; Shenandoah Natl. Pk. WEST VIRGINIA: Pocahontas Co.

A. chandleri—CALIFORNIA: Mariposa Co.

A. chloris—GEORGIA: Bartow Co. KENTUCKY: Menifee Co. MASSACHUSETTS: Willard Brook St. Forest. NEW HAMPSHIRE: Coos Co. NEW YORK: Tompkins Co.; Adirondack Pk. NORTH CAROLINA: Buncombe Co. NOVA SCOTIA: Victoria; Chester Basin; Wentworth. OHIO: Geauga, Portage Cos. PENNSYLVANIA: Lincoln Falls. QUEBEC: Knowlton; R. Pelletier. TENNESSEE: Great Smoky Mts. Natl. Pk. VIRGINIA: Craig, Giles, Montgomery, Shenandoah Cos. WEST VIRGINIA: Pocahontas, Pendleton Cos.

A. concolor—NEW BRUNSWICK: Chatham. NEWFOUNDLAND: Cormack; Kitty's Brook; Spruce Brook. NEW HAMPSHIRE: Coos, Grafton Cos. NEW YORK: Adirondak Pk. ONTARIO: Durham, Peel Cos. PENNSYLVANIA: Monroe Co. QUEBEC: Gaspé Pen.; Pk. Mt. Tremblant. VERMONT: Washington Co.

A. delicata—CALIFORNIA: Humboldt, Mendocino, Sonoma Cos. OREGON: Benton, Clackamas, Clatsop, Hood River, Polk, Tillamook, Union Cos.

A. fraterna—BRITISH COLUMBIA: Squamish; Vancouver; Vedder Crossing. CALIFORNIA: Butte, Contra Costa, Marin, Napa, Nevada, Plumas, Santa Clara, Santa Cruz, Shasta, Sierra, Siskiyou, Tehama Cos. OREGON: Benton, Clatsop, Douglas, Hood River, Jackson, Lane, Multinomah Cos. WASHINGTON: Clallam, Jefferson, Mason Cos.

A. furcula—SOUTH CAROLINA: Aiken Co.

A. hamata—ALABAMA: Jackson Co.

A. idei—GEORGIA: Bartow Co. MAINE: Washington Co. OHIO: Pickaway Co. QUEBEC: Pk. Mt. Tremblant; South Boulton. VIRGINIA: Fairfax Co.

A. imbecilla—OHIO: Geauga Co. PENNSYLVANIA: Beaver, Forest. Northampton Cos. VIRGINIA: Augusta, Bath, Shenandoah Cos. WEST VIRGINIA: Pocahontas, Summers Cos.

A. leonarda—MAINE: Washington Co. MICHIGAN: Houghton Co. MINNESOTA: Koochiching, Lake, Pine Cos. QUEBEC: R. Nabisipi.

A. medveda—ALBERTA: Waterton Lakes Natl. Pk. BRITISH COLUMBIA: Fernie; Kamloops. IDAHO: Boise, Lemhi Cos. MONTANA: Carbon, Cascade, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lincoln, Meagher, Missoula, Ravalli, Stillwater Cos. WYOMING: Grand Teton, Yellowstone Natl. Pks.

A. nanina—NORTH CAROLINA: Buncombe Co. TENNESSEE: Great Smoky Mts. Natl. Pk. VIRGINIA: Smyth Co.

A. natchez—MISSISSIPPI: Claiborne, Simpson Cos.

A. neglecta—NORTH CAROLINA, TENNESSEE: Great Smoky Mts. Natl. Pk.

A. pilosa—COLORADO: Clear Creek, Grand, Larimer Cos.

A. roberti—ILLINOIS: Rock Island Co.

A. serrata—ALASKA: Anchorage; Kenai Pen.; Kodiak Isl.; Tom's Village. ALBERTA: Banff, Waterton Lakes Natl. Pks. BRITISH COLUMBIA: Lemon Crk.; Summit L.; Upper Peace R.; Vedder Crossing. IDAHO: Blaine, Boise, Shoshone Cos. MONTANA: Carbon, Cascade, Deer Lodge, Flathead, Gallatin, Glacier, Granite, Missoula, Park, Ravalli, Sweet Grass Cos. WASHINGTON: Whatcom Co.; Olympic Natl. Pk. YUKON: Swift R.

A. severa—ALASKA: Alaskan Pen.; Brooks Range; Chatanika R.; Katmai Natl. Mon.; Kenai Pen.; Kodiak Isl.; Palmer; Pr. of Wales Isl.; Seward Pen. ALBERTA: Banff, Waterton Lakes Natl. Pks.; Edson. BRITISH COLUMBIA: Babine; Columbia Mts.; François L.; Kootenay Natl. Pk.; Terrace; Vancouver Isl.; Vedder Crossing. CALIFORNIA: Wadell Crk. COLORADO: Routt Co. IDAHO: Blaine, Custer, Franklin, Lemhi Cos. MONTANA: Beaverhead, Big Horn, Cascade, Deer Lodge, Fergus, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lake, Lincoln, Meagher, Missoula, Park, Ravalli, Stillwater, Sweet Grass Cos. NEVADA: Elko, White Pine Cos. OREGON: Benton, Clatsop, Curry, Jackson Cos. UTAH: Cache, Davis, Morgan, Salt Lake, Summit, Tooele, Utah, Wasatch, Washington, Weber Cos. WASHINGTON: Clallam, Cowlitz, Jefferson, King, Mason, Thurston Cos. WYOMING: Big Horn, Fremont, Lincoln, Sheridan, Sublette, Sweetwater Cos.; Yellowstone Natl. Pk. YUKON: Upper Laird R.

A. usa—GEORGIA: Dawson, Habersham Cos. NORTH CAROLINA: Buncombe, McDowell, Yancey Cos. OHIO: Lake Co. PENNSYLVANIA: Westmoreland Co. SOUTH CAROLINA: Oconee Co. TENNESSEE: Great Smoky Mts. Natl. Pk. VIRGINIA: Augusta,

Bath, Botetourt, Giles, Logan, Madison, Montgomery, Rockbridge, Rockingham, Shenandoah, Smyth Cos.; Shenandoah Natl. Pk. WEST VIRGINIA: Logan, Pocahontas, Randolph Cos.

A. voinae—NEW YORK: Keene. NOVA SCOTIA: Baddeck; Wentworth.

A. vostoki—NEW YORK: Wyoming Co. NOVA SCOTIA: Baddeck; Wentworth; Victoria. PENNSYLVANIA: Erie Co.

DISCUSSION

Alloperla adults are usually distinguished from *Bisancora* and *Sweltsa* by the green color, *in vivo*, and paucity of heavy sclerotization and dark markings (Figs. 3, 4, 5). Although both male epiprocts and female subgenital plates vary widely among species, brevity of the epiproct tip, absence of tergal ridges and a generally broad, flattened subgenital plate that does not swell up anteriorly on sternum 8 differentiate *Alloperla* adults from the rest of the tribe (Figs. 64–66, 70–73, 75, 80, 82–84, 89–90). The maxillary comb and streamlined shape of *Alloperla* larvae are unique within the subfamily (Figs. 35, 36, 74). Comparatively fewer corporal setae and presence of intrasegmental cercal hairs are also characteristic of *Alloperla* alone, among Chloroperlinae genera with known larvae (Figs. 26, 46). Slight elongation of the occipital area posterior to the compound eyes is distinctive in many *Alloperla* species and is reminiscent of the Paraperlinae (Figs. 3, 74).

Larvae are frequently found inhabiting hyporheal situations (J. A. Stanford, personal communication; Hynes, 1976; personal observation), for which they are apparently well suited, as evidenced by short legs, elongate body, and minimal setation (Fig. 74). Prior to emergence, they are often collected in gravel, on moss and under bark of submersed wood in clean swift streams and springs. *Alloperla* is generally less commonly collected than *Sweltsa* larvae or adults, unless the brief peak of emergence is encountered. As in most Chloroperlinae, adults flutter to and rest on streamside vegetation.

Sweltsa Ricker

Alloperla (*Sweltsa*) Ricker, 1943: 135. Type species: *Sweltsa oregonensis* (Frison).

Sweltsa—Illies, 1966: 450.

DESCRIPTION

Adult

Body length 8 to 18 mm. Yellow, tan, or fuscous, frequently strongly sclerotized; generally pale with very dark markings that include ocellar rings, pronotal stripes or margin, reticulate markings, sutures, medial and brief lateral longitudinal abdominal stripes; often with dark or dusky shadings on meso- and metanota, thoracic sterna, abdominal sclerites, tarsal apices, basal and terminal antennal segments, wing veins. Head with compound eyes set near posterior corners and occiput abruptly tapered posteriorly; heavily rugose areas on occiput, frons; mandibles with 4 or 5 sclerotized teeth. Pronotum rectangular; corners rounded; width equaling head width. Wings hyaline with forewing A2 branched; folded hindwing anal area with 3 veins; Rs of fore- and hindwing branched beyond cord; usually macropterous, sometimes brachypterous in springs, at high altitudes. Mesosternal Y-ridge unmodified. Terminal abdominal segments with lateral brushes of multiple hairs; hammer absent; up to 7 abdominal segments with pleural folds. Cerci unmodified; 10–12 segments. (Figs. 1, 2, 4, 19, 25, 63; *see also* 14, 16)

Male

Tergum 9, sometimes 8, strongly indented posterior to transverse, anteriorly sclerotized, scalloped ridge located anteriorly or medially on tergum; ridge ¼ width of tergum, attached to transverse, lightly sclerotized band at anterior of tergum; hemiterga 10 unmodified; transverse bands thick, sclerotized. Epiproct erectile, moderately to heavily sclerotized, nearly hidden when relaxed in often large, cup-like basal anchor and membranous groove between hemiterga; anal lobe inconspicuous. Epiproct tip hinged, recurved anteriorly, large, extending beyond tergum 10; variously inflated, highly sculptured, tongue-like or digitate; finely setose, often heavily sclerotized; cowl not enlarged. Basal bar concave ventrally, as thick as, or thicker than, and not fused with, paragenital plates. Basal anchor set on anterior margin tergum 10, often extending far into indented area of tergum 9; as long as, to longer than, wide; ½ width tergum. Membranous aedeagus tubular basally, extending to swollen or enlarged, dish-faced apex with 2 small posterior, 2 large anterior lobes; occasionally with delicate to strongly sclerotized, striate leaflets. (Figs. 75–80)

Female

Sternite 9 concave, sparsely setose. Subgenital plate variously shaped and setose, usually lozenge- or pillow-shaped with rounded, blunt or emarginate flap covering genital pore and overlapping much of sternum 9; apparently arising and swollen from middle of sternum 8, especially obvious in lateral aspect; plate width ½ to ¾ segment width; lateral indentations evident at termination of posterior segmental fringe where free posterior flap of plate appears to overlap segmental margin; plate often accentuated by dark shading of slightly heavier sclerotized areas; setae longest on most convex and most posterior parts of plate. Sternum 10 frequently with pair of sclerotized dusky patches laterally. Vagina membranous. (Figs. 72, 73)

Larva

To 18 mm. Tan to light fuscous, concolorous, or with pale areas. Head with compound eyes set near posterior corners and occiput abruptly tapered posteriorly. Maxilla terminating in single large tooth and penultimate small tooth; dorsal aspect of paraglossa usually with thick row of staggered bristles on inner margin, scattered bristles on remainder of surface. Pronotum nearly oval or rectangular, corners rounded; width equaling, to slightly greater than, head width; fringe broken on lateral margins, shorter hairs more numerous on anterior angles, longer hairs most numerous, evenly spaced posteriorly. Wingpads convex on outer margins, oblique on inner margins. Mesosternal Y-ridge unmodified. Slightly broader, flattened abdomen, wingpads, pronotum, yielding more "perlid" habitus than other genera. Clothing hairs thick, often dark; bristle fringe thick and long hairs numerous on posterior abdominal tergal margins. Cerci fringed with several dorsal and ventral or partial whorls of hairs extending posteriorly from posterior margin of each segment; these hairs generally longer than segment on posterior half of cerci; 10–16 segments. (Figs. 27, 34, 40, 47, 81)

Ovum

Ovoid to skewed ovoid, circular cross section; golden tan to brown; chorion finely to grossly punctate. Collar, when present, flanged, incised, with short stalk or none; often surrounded by smooth halo basally (Figs. 56, 57).

DISTRIBUTION AND NEARCTIC SPECIES LIST: *Sweltsa* Ricker

Eastern, western Nearctic, 5 eastern Palearctic species.

albertensis (Needham and Claassen) 1925, northern Rocky Mts.
borealis (Banks) 1895, western Nearctic.
californica (Jewett) 1965, California.
coloradensis (Banks) 1898, Rocky Mts., Pacific Northwest.
continua (Banks) 1911, California.
exquisita (Frison) 1935a, Pacific Northwest.
fidelis (Banks) 1920, northern, central Rocky Mts., Pacific Northwest.
gaufini Baumann 1973, Idaho-Utah border.
lamba (Needham and Claassen) 1925, central Rocky Mts., Oregon.
lateralis (Banks) 1911, eastern Nearctic.
mediana (Banks) 1911, southern Appalachian Mts.
naica (Provancher) 1876, eastern Canada south to West Virginia.
occidens (Frison) 1937, Pacific Northwest.
onkos (Ricker) 1935b, northeastern Nearctic.
oregonensis (Frison) 1935a, Pacific Northwest.
pacifica (Banks) 1895, Pacific Northwest to California.
revelstoka (Jewett) 1955, northern Rocky Mts., Oregon, Washington.
tamalpa (Ricker) 1952, California.
townesi (Ricker) 1952, California.
urticae (Ricker) 1952, southern Appalachian Mts.

MATERIAL EXAMINED

Sweltsa albertensis—ALBERTA: Waterton Lakes Natl. Pk. BRITISH COLUMBIA: Vancouver Isl. IDAHO: Blaine, Custer, Latah, Lemhi Cos. MONTANA: Broadwater, Carbon, Cascade, Deer Lodge, Flathead, Gallatin, Glacier, Granite, Judith Basin, Meagher, Missoula, Park, Ravalli, Stillwater, Sweet Grass Cos. WYOMING: Park Co.; Yellowstone Natl. Pk.

S. borealis—ALASKA: Fairbanks; Little Port Walker; Sashin Crk. ALBERTA: Banff, Waterton Lakes Natl. Pks.; Kanaskis Hwy. BRITISH COLUMBIA: Albirni; Atlin; Creston; Hemlock; Kamloops; King Isl.; Lakelse; Purcell Mts.; Queen Charlotte Isl.; Sproul; Vancouver Isl.; Vedder Crossing. CALIFORNIA: Marin, Mono, Nevada,

Plumas, Shasta, Sierra, Siskiyou, Tuolumne Cos.; Yosemite Natl. Pk. COLORADO: Boulder, Clear Creek, El Paso, Grand, Hinsdale, La-Plata, Larimer, Mesa, Pitkin, Summit Cos. IDAHO: Blaine, Boise, Bonner, Franklin, Lemhi Cos. MONTANA: Carbon, Cascade, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lake, Lincoln, Missoula, Park, Ravalli, Sweet Grass Cos. OREGON: Baker, Benton, Clackamas, Clatsop, Grant, Hood River, Jackson, Jefferson, Klamath, Lincoln, Multnomah, Union, Wasco Cos. UTAH: Cache, Duchesne, Salt Lake, Sevier, Utah, Wasatch, Washington, Weber Cos. WASHINGTON: Asotin, Chelan, Clallam, Grays Harbor, Jefferson, King, Pierce Cos. WYOMING: Albany, Big Horn, Park, Sheridan, Teton Cos. YUKON: Whitehorse.

S. coloradensis—ALBERTA: Banff, Jasper, Waterton Lakes Natl. Pks.; Foster; Kanaskis Hwy.; Laggan; Radnor. ARIZONA: Apache Co. BRITISH COLUMBIA: Atlin; Babine; François L.; Quesnel; Wells Gray Prov. Pk. CALIFORNIA: El Dorado, Placer Cos. COLORADO: Arapahoe, Boulder, Clear Creek, Conejos, Dolores, Eagle, El Paso, Garfield, Grand, Gunnison, Hinsdale, Jackson, Lake, Larimer, Mineral, Montrose, Park, Routt, Saguache, Summit Cos. IDAHO: Adams, Blaine, Bonneville, Custer, Elmore, Franklin, Idaho, Lemhi, Valley Cos. MONTANA: Carbon, Cascade, Flathead, Gallatin, Glacier, Golden Valley, Lake, Lincoln, Madison, Meagher, Missoula, Ravalli, Stillwater, Sweet Grass, Wheatland Cos. NEVADA: Elko, White Pine Cos. NEW MEXICO: Catron, Colfax, Rio Arriba, San Miguel, Santa Fe, Taos Cos. OREGON: Benton, Clatsop, Coos, Crook, Douglas, Grant, Harney, Klamath, Marion, Polk, Union, Wallowa, Washington, Yamhill Cos. UTAH: Box Elder, Cache, Daggett, Davis, Duchesne, Morgan, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Utah, Weber Cos. WASHINGTON: King, Yakima Cos. WYOMING: Albany, Big Horn, Carbon, Fremont, Lincoln, Park, Sublette, Teton Cos. YUKON: Dawson.

S. continua—CALIFORNIA: Los Angeles, Riverside, San Bernardino Cos.

S. exquisita—ALASKA: Pipeline Crk. BRITISH COLUMBIA: Albirni; Klaskish Inlet; Liumchin; Queen Charlotte Isl.; Tyce; Vancouver Isl.; Vedder Crossing. OREGON: Benton, Clackamas, Hood River, Jackson, Jefferson, Josephine, Lane Cos. WASHINGTON: Clallam, Jefferson, King, Kittitas, Mason, Pierce, Snohomish, Yakima, Whatcom Cos.

S. fidelis—ALBERTA: Banff, Waterton Lakes Natl. Pks.; Divided L.; Jacques L.; L. Louise; Moraine L. BRITISH COLUMBIA: Glacier; Kamloops; Laird Hot Spr.; Mt. Revelstoke Natl. Pk.; Pine Valley; Vancouver Isl.; Wells. CALIFORNIA: Del Norte Co. COLORADO: Larimer Co. IDAHO: Blaine, Boise, Butte, Custer, Fremont, Idaho, Kootenai, Latah, Shoshone Cos. MONTANA: Beaverhead, Broadwater, Carbon, Cascade, Flathead, Gallatin, Glacier, Granite, Judith Basin, Lake, Lincoln, Meagher, Mineral, Missoula, Park, Powell, Ravalli, Sweet Grass Cos. OREGON: Baker, Benton, Clatsop, Curry, Douglas, Jackson, Lincoln, Umatilla, Union, Yamhill Cos. WASHINGTON: Asotin, Pend Oreille, Pierce, Spokane, Whitman Cos. WYOMING: Park, Sublette, Teton Cos. YUKON: Whitehorse.

S. gaufini—IDAHO: Franklin Co. UTAH: Box Elder, Cache Cos.

S. lamba—COLORADO: Boulder, Clear Creek, Delta, Eagle, El Paso, Garfield, Grand, Lake, Larimer, Pitkin, Routt, Summit Cos. IDAHO: Fremont, Teton Cos. OREGON: Baker, Grant, Klamath, Union Cos. UTAH: Box Elder, Cache, Davis, Rich, Salt Lake, San Juan, Summit, Wasatch, Washington, Weber Cos. WYOMING: Albany, Lincoln Cos.

S. lateralis—CONNECTICUT: New Haven Co. GEORGIA: Dawson Co. MARYLAND: Frederick Co. MASSACHUSETTS: Franklin Co. NEW BRUNSWICK: Chatham. NEW HAMPSHIRE: Coos, Grafton Cos. NEW YORK: Adirondack Pk.; Essex. NORTH CAROLINA: Buncombe, Macon, Yancey Cos.; Great Smoky Mts. Natl. Pk. PENNSYLVANIA: Centre, Elk, Fayette, Forest, Fulton, Somerset, Westmoreland Cos. QUEBEC: Gaspé Pen.; Ste. Petronille. SOUTH CAROLINA: Oconee Co. TENNESSEE: Great Smoky Mts. Natl. Pk. VERMONT: Bolton. VIRGINIA: Augusta, Bath, Floyd, Giles, Madison, Nelson, Patrick, Rappahannock, Rockbridge, Rockingham, Shenandoah, Smyth Cos.; Shenandoah Natl. Pk. WEST VIRGINIA: Greenbrier, Hampshire, Hardy, Nicholas, Pendleton, Pocahontas, Preston, Randolph, Tucker Cos.

S. mediana—NORTH CAROLINA: Buncombe, Swain, Yancey Cos.; Great Smoky Mts. Natl. Pk. TENNESSEE: Scott Co.; Great Smoky Mts. Natl. Pk. VIRGINIA: Grayson, Smyth Cos.

S. naica—NEWFOUNDLAND: Big Falls; Birchey; Cape Ray; Cartwright; Labrador. NEW HAMPSHIRE: Coos, Grafton Cos. NEW YORK: Essex Co.; Adirondack Pk. PENNSYLVANIA: Monroe, Westmoreland Cos. QUEBEC: Bradore Bay; Castor R.; Chicoutimi; Gaspé

Pen.; Matamek; Pk. Mt. Tremblant; Sept Iles. VERMONT: Orange Co. WEST VIRGINIA: Pocahontas Co.

S. occidens—BRITISH COLUMBIA: Liumchin; Vedder Crossing. IDAHO: Shoshone Co. OREGON: Benton, Clackamas, Hood River Cos. WASHINGTON: Lewis, Pierce Cos.

S. onkos—CONNECTICUT: Litchfield Co. DELAWARE: New Castle Co. MAINE: Washington Co. MARYLAND: Frederick Co. MASSACHUSETTS: Hampshire Co. NEW HAMPSHIRE: Coos, Grafton, Merrimack Cos. NEW YORK: Essex, Tompkins Cos.; Adirondack Pk. NOVA SCOTIA. OHIO: Athens, Geauga Cos. ONTARIO: Dufferin, Durham, Halton Cos.; Muskoka; Singhampton; Algonquin Prov. Pk. PENNSYLVANIA: Beaver, Chester, Erie, Fayette, Luzerne, Lycoming, Monroe, Northampton, Westmoreland Cos. QUEBEC: Gaspé Pen.; Gatineau Pk.; Glen Sutton; Ile d'Orléans; Matamek R.; Mt. St. Hilaire; Pk. Mt. Tremblant; Ruis Beattie; St. Hippolyte. VERMONT: Orange, Washington, Windsor Cos. VIRGINIA: Alleghany, Augusta, Bath, Craig, Dickenson, Giles, Grayson, Hanover, Madison, Montgomery, Nelson, Page, Rappahannock, Rockingham, Shenandoah, Tazewell, Washington Cos.; Shenandoah Natl. Pk. WEST VIRGINIA: Fayette, Greenbrier, Logan, Monongalia, Nicholas, Pendleton, Pocahontas, Randolph, Tucker, Wayne Cos.

S. oregonensis—ALASKA: Juneau. BRITISH COLUMBIA: Lakelse R.; Vancouver Isl.; Vedder Crossing. OREGON: Benton, Clackamas, Clatsop, Douglas, Hood River, Lane Cos. WASHINGTON: Clallam, Grays Harbor, King, Mason, Pierce, Yakima Cos.

S. pacifica—BRITISH COLUMBIA: Quesnel; Vancouver Isl.; Vedder Crossing. CALIFORNIA: Fresno, Lake, Los Angeles, Marin, Nevada, Riverside, San Bernardino, Shasta, Sierra, Trinity, Tulare Cos.; Yosemite Natl. Pk. OREGON: Benton, Clackamas, Clatsop, Curry, Douglas, Jackson, Josephine, Klamath, Lincoln, Polk, Tillamook Cos. WASHINGTON: Clallam, Kittitas, Thurston Cos.

S. revelstoka—ALBERTA: Banff, Waterton Lakes Natl. Pks. BRITISH COLUMBIA: Kootenay, Mt. Revelstoke Natl. Pks.; Liumchin; Slocan City. MONTANA: Flathead, Gallatin, Glacier, Lake, Ravalli, Sanders, Sweet Grass Cos. OREGON: Clackamas, Hood River Cos. WASHINGTON: Mt. Rainier Natl. Pk. WYOMING: Yellowstone Natl. Pk.

S. tamalpa—CALIFORNIA: Marin, San Benito, Santa Clara Cos.

S. townesi—CALIFORNIA: El Dorado, Glenn, Mono, Nevada, Plu-

mas, Riverside, Shasta, Sierra, Tehama, Tuolumne Cos.; Yosemite Natl. Pk.

S. urticae—NORTH CAROLINA: McDowell Co.; Great Smoky Mts. Natl. Pk. VIRGINIA: Floyd, Grayson, Patrick, Smyth Cos.

DISCUSSION

Dark occipital and thoracic markings and abdominal stripes generally distinguish adult *Sweltsa* from *Bisnacora* and *Alloperla* (Figs. 3–5). Large epiproct tip and tergal ridge in males and swollen or emarginate subgenital plate in females also differentiate *Sweltsa* (Figs. 72, 73, 75, 79, 80) from the remainder of the tribe (Figs. 64–67, 70, 71, 82–84, 89, 90). A more flattened "perlid" shape, combined with thick body and cercal setation are characteristic of the larvae (Figs. 27, 47, 81). The largest Chloroperlinae adults and larvae are included in the genus.

Sweltsa adults and larvae are the most commonly collected Chloroperlidae. Apparently the least prone to subterranean existence, *Sweltsa* larvae are generally collected over a longer yearly interval than are other chloroperlids. Although most species inhabit clean swift streams, some populations live in springs and cold, high-altitude lakes. Various degrees of brachyptery (Fig. 25) have been discovered in spring and lake populations of *Sweltsa fidelis*, *S. revelstoka*, *S. borealis* and *S. lamba*.

Bisancora Surdick

Bisancora Surdick, 1981: 356. Type species: *Bisancora rutriformis* Surdick.

DESCRIPTION

Adult

Body length 4 to 6 mm. Yellowish tan or pale fuscous, moderately sclerotized; generally dusky with dark ocellar rings and dark or dusky markings on head, lateral angles of occiput, ocellar triangle to clypeus, frons, base and distal ¾ antennae, anterior and posterior margins and median of pronotum, sutures, thoracic nota and sterna, rugosities, wing veins, medial and brief lateral abdominal stripes. Head with compound eyes set near posterior corners and occiput abruptly

tapered posteriorly; mandibles with sclerotized teeth. Pronotum square, lightly rugose, narrower than head width; thick, even margins; corners rounded. Wings hyaline with forewing A2 branched; folded hindwing anal area with 3 veins; Rs of fore- and hindwing branched beyond cord; macropterous. Mesosternal Y-ridge with medial ridge extending nearly to costa. Terminal abdominal segments with lateral brushes of multiple hairs; hammer absent; up to 7 abdominal segments with pleural folds. Cerci unmodified; 10 segments. (Figs. 5, 15; *see also* 16, 19)

Male

Tergum 9 indented slightly at median of posterior margin, otherwise unmodified. Hemiterga 10 unmodified; transverse bands sclerotized, thick. Epiproct erectile, moderately sclerotized, nearly hidden when relaxed in membranous groove between hemiterga; anal lobe inconspicuous. Epiproct tip hinged, recurved anteriorly, not extending beyond tergum 10; variously flattened and curved or curled; lightly to moderately sclerotized; cowl not enlarged. Basal bar concave ventrally, as wide as, or slightly wider than, unconnected paragenital plates. Basal anchor sequentially double; posterior anchor ⅓ segment width; anterior anchor ½ segment width, not extending anteriorly beyond transverse bands of hemiterga. Aedeagus terminating in 2 lightly sclerotized dorsal flaps or leaflets and 2 ventral membranous digits. (Figs. 82–88)

Female

Sternite 9 slightly concave, sparsely setose. Subgenital plate scalloped, pillow-shaped, arising from middle to anterior of sternum 8, covering genital pore, hardly overlapping sternum 9; plate distinct from remainder of sternum by darker sclerotization and indented, membranous, setaeless circumference; lateral indentations evident at termination of posterior segmental fringe where free posterior flap of plate appears to overlap segmental margin; plate ½ to ¾ sternum width; central scallop evenly setose; lateral scallops with long, dense hairs. Vagina thickened, not sclerotized. (Figs. 80, 90)

Larva

Unknown.

Ovum

Ovoid, circular cross section; chorion finely punctate; without collar. (*See* Figs. 54–57 for similar ova.)

DISTRIBUTION AND SPECIES LIST: *Bisancora* Surdick

Western Nearctic.

pastina (Jewett) 1962, California, Oregon.
rutriformis Surdick 1981, California.

MATERIAL EXAMINED

Bisancora pastina—CALIFORNIA: Del Norte, Napa Cos.
B. rutriformis—CALIFORNIA: Alameda, Los Angeles Cos.

DISCUSSION

Small size, tan pigmentation, and square pronotum readily distinguish *Bisancora* (Fig. 5) from *Sweltsa* (Fig. 4) and most *Alloperla* (Fig. 3). The uniquely flattened and curled, rather than three-dimensional, epiproct tip (Figs. 82–84, 88), and the swollen, scalloped female subgenital plate (Figs. 89, 90) characterize the adults. Both species are relatively rare or, at most, only locally common.

Suwalliini New Tribe

Epiproct tip a hairy membranous knob; basal anchor, bar and paragenital plates fused to form star-shaped plate; anal lobe small. Hemitergal processes developed on segment 10. Aedeagus spinulated. Vagina membranous. Adult mandibles reduced.

Suwalliini includes the genera *Suwallia* Ricker and *Neaviperla* Ricker, and is represented in the eastern and western Nearctic and the eastern Palearctic.

Suwallia Ricker

Alloperla (*Suwallia*) Ricker, 1943: 139. Type species: *Suwallia pallidula* (Banks).

Suwallia—Illies, 1966: 449.

DESCRIPTION

Adult

Body length 6 to 10 mm. Yellow to light fuscous, moderately sclerotized; generally pale with dark ocellar rings, sutures; dusky to dark pronotal margin, basal and apical antennal segments, median and brief lateral longitudinal abdominal stripes, tarsal apices, sometimes head and pronotal rugosities, thoracic sclera. Head with compound eyes set near posterior corners and occiput tapering abruptly posteriorly; mandibles without numerous sclerotized teeth but terminating in 2 or 3 small, lightly sclerotized teeth and penultimate, hirsute, membranous knob. Pronotum rectangular; corners rounded; width equaling head width; lateral margins narrow. Wings hyaline with forewing A2 branched; folded hindwing anal area with 3 veins; Rs of fore- and hindwing branched beyond cord; macropterous. Mesosternal Y-

ridge unmodified. Terminal abdominal segments with evenly spaced long setae on lateral margins, lacking brushes of multiple hairs; hammer absent; abdominal pleural folds absent beyond segment 2. Cerci unmodified except for inconspicuous but thick, ventrally pointing hair apically on each segment; 8–10 segments. (Figs. 6, 17; *see also* 14, 19)

Male

Tergum 9 slightly produced posteriorly; hemiterga 10 modified posteriorly into setose, medially directed, digitate processes; transverse bands sclerotized, very thick. Epiproct somewhat erectile, partially moderately sclerotized; nearly hidden beneath hemiterga and under posterior extension of tergum 9 when tergum 10 tilts dorsoanteriorly on relaxed abdomen; anal lobe small. Epiproct tip not hinged, not recurved; an inconspicuous membranous, variously hirsute small knob or button; cowl not enlarged. Basal bar, anchor and reduced paragenital plates merged to form starlike basal plate; basal plate scarcely cupped, with scattered setae proximally, extending anteriorly to transverse bands, ¼ to ⅓ tergum width at widest. Aedeagus tubular, terminating in brief lateral lobes, dorsal pointed and anteriorly directed lobe, thickened penis head; membranous with fine colorless to prominent golden spinulae, particularly dorsally, in various arrays. (Figs. 91–95)

Female

Sternite 9 slightly concave, sparsely setose. Subgenital plate rounded, tapered or squared on posterior margin; flattened ventrally, often with distal portion tilted slightly ventrad (evident in lateral aspect); base arising medially on sternum 8, outlined by indentation and interruption of setation on sternum, particularly where free flap begins anterior to and overlapping posterior margin of sternum 8; flap longer than base, covering genital pore and extending over sterna 9 and 10; posterior margin bearing long, scattered setae. Vagina membranous. (Figs. 96, 97)

Larva

To 10 mm. Tan to light fuscous, with indistinct pale areas. Head with compound eyes set near posterior corners and occiput abruptly tapered posteriorly. Maxilla terminating in single, large tooth and

penultimate small tooth; dorsal aspect of paraglossa generally with single regular row of distinct, thick hairs on inner margin, scattered hairs on remainder of surface. Pronotum rectangular; corners rounded; width equaling head width; fringe interrupted laterally, with numerous long hairs anteriorly and posteriorly, but not as regular as in *Sweltsa*, *Triznaka*. Wingpads convex on lateral margins, oblique on inner margins. Mesosternal Y-ridge unmodified. Clothing, long fine, and bristle fringe hairs numerous but not as regular or abundant as in *Sweltsa* and *Triznaka*. Cerci with one each dorsal and ventral long fine hairs extending obliquely posterior from posterior margin of each segment; these hairs just shorter than, to as long as, segment on posterior half of cerci; 13–15 segments. (Figs. 28, 41, 48, 98; *see also* 34)

Ovum

Ovoid, swollen at equator yielding diamond profile; circular cross section; light fuscous to golden brown; chorion finely punctate or reticulate on anterior ⅔, especially at equator, but not much beyond posterior ring of micropyles. Collar usually present, covering most of anterior pole, stalked or unstalked, incised, flanged. (Figs. 60, 61)

DISTRIBUTION AND NEARCTIC SPECIES LIST: *Suwallia* Ricker

Eastern, western Nearctic; 8 eastern Palearctic species.

autumna (Hoppe) 1938, western Nearctic.
dubia (Frison) 1935a, western Nearctic.
lineosa (Banks) 1918, western Nearctic.
marginata (Banks) 1897, eastern Nearctic.
pallidula (Banks) 1904, western Nearctic.

MATERIAL EXAMINED

Suwallia autumna—BRITISH COLUMBIA: Vedder Crossing. CALIFORNIA: Nevada Co.; Yosemite Nal. Pk. COLORADO: Rocky Mt. Natl. Pk. IDAHO: Lemhi Co. MONTANA: Flathead, Gallatin, Glacier, Lake, Missoula, Powell Cos. OREGON: Clackamas, Clatsop, Lane, Yamhill Cos. WASHINGTON: King, Kittitas Cos.

S. dubia—ALASKA: Wrangell. ALBERTA: Waterton Lakes Natl. Pk. BRITISH COLUMBIA: Hope; Vancouver Isl.; Vedder Crossing. COLORADO: Eagle Co. IDAHO: Blaine, Bonner, Camas, Franklin

Cos. MONTANA: Flathead, Glacier, Missoula, Powell, Ravalli Cos. OREGON: Clatsop, Hood River, Klamath, Wallowa Cos. UTAH: Cache, Davis, Morgan, Salt Lake Cos. WASHINGTON: Grays Harbor, Jefferson, Kittitas, Madison Cos. WYOMING: Park Co.

S. lineosa—ALBERTA: Banff, Jasper, Waterton Lakes Natl. Pks. BRITISH COLUMBIA: Kamloops. IDAHO: Custer, Shoshone Cos. MONTANA: Carbon, Flathead, Gallatin, Glacier, Lake, Missoula, Park, Ravalli Cos. OREGON: Baker Co. UTAH: Cache, Morgan Cos. WYOMING: Grand Teton Natl. Pk.

S. marginata—GEORGIA: White Co. MAINE: Piscataquis Co. NEW HAMPSHIRE: Grafton Co. NEW YORK: Tompkins Co. NORTH CAROLINA: Yancey Co.; Great Smoky Mts. Natl. Pk. ONTARIO: Credit R.; Terra Cotta. PENNSYLVANIA: Jefferson, Somerset, Westmoreland Cos. QUEBEC: Bradore Bay; Gaspe Pen.; Glen Sutton; Pk. Mt. Tremblant. TENNESSEE: Great Smoky Mts. Natl. Pk. VERMONT: Chittenden, Lamoille Cos. VIRGINIA: Craig, Giles, Grayson, Hanover Cos. WEST VIRGINIA: Pendleton, Randolph Cos.

S. pallidula—ALASKA: Anatuvuk Pass; Kenai Pen.; Kodiak Isl.; Mt. McKinley Natl. Pk.; North Slope; Ranchera R.; Seward Pen. ALBERTA: Banff, Jasper, Waterton Lakes Natl. Pks. ARIZONA: Apache Co. BRITISH COLUMBIA: Babine; Bowron Lake Prov. Pk.; Douglas Lake; Nicola Lake; Prince George; Quesnel; Slocan; Vedder Crossing. CALIFORNIA: Alameda, Nevada, Plumas, Santa Clara, Shasta, Sierra, Tehama Cos. COLORADO: Boulder, Chaffee, Clear Creek, El Paso, Garfield, Gilpin, Gunnison, Hinsdale, Larimer, Las Animas, Moffat, Ouray, Park, Pitkin, Routt, Summit Cos. IDAHO: Blaine, Camas, Custer, Franklin, Fremont, Lemhi Cos. MONTANA: Beaverhead, Big Horn, Cascade, Deer Lodge, Flathead, Gallatin, Glacier, Golden Valley, Granite, Gunnison, Jefferson, Judith Basin, Lake, Lincoln, Madison, Meagher, Missoula, Park, Pondera, Ravalli, Stillwater, Sweet Grass, Wheatland Cos. NEW MEXICO: Taos Co. NEVADA: Washoe Co. OREGON: Clatsop, Hood River, Josephine, Lincoln, Union Cos. UTAH: Beaver, Cache, Daggett, Davis, Duchesne, Rich, Salt Lake, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, Washington, Weber Cos. WASHINGTON: Jefferson, Kittitas, Mason, Pierce, Thurston Cos. WYOMING: Albany, Park, Teton, Sublette Cos.

DISCUSSION

Adult males of *Suwallia* are distinctive among Nearctic Chloroperlidae because of the digitate hemitergal processes (Figs. 91, 92). Except for unmodified cerci, they could be confused only with *Neaviperla* (Figs. 99–102). Adult female *Suwallia*, however, are more easily confused with other genera. The absence of brushes on terminal abdominal segments distinguishes them from *Alloperla* (Figs. 71, 97), and the U scutoscutellar suture marks (Fig. 6) separate them from *Triznaka* (Fig. 8) and *Neaviperla* (Fig. 7), both with W thoracic marks. The large, flat, free flap of the subgenital plate is an additional clue to identity (Figs. 96, 97). In other Chloroperlinae the posterior portion of the plate is usually more swollen, and not as extensive. Adult *Suwallia* and *Neaviperla* are the only Chloroperlinae with reduced mandibles (Figs. 17, 18). Larvae are similar to *Sweltsa*, but slightly less flattened and broad, and less hirsute (Figs. 81, 98). Setation of the paraglossae may be variable (Fig. 41).

Western Nearctic *Suwallia* species are generally common, although the only eastern species, *S. marginata*, is relatively infrequently collected. Subtle differences in morphology among species accompany more obvious gradations in emergence times, coloration, and geographical distribution. The aedeagus must be examined in order to determine some males; females have not been adequately associated in the Nearctic species.

Neaviperla Ricker

Alloperla (*Neaviperla*) Ricker, 1943: 141. Type species: *Neaviperla forcipata* (Neave).

Neaviperla—Illies, 1966: 448.

DESCRIPTION

Adult

Body length 9 to 10 mm. Yellow to light tan, moderately sclerotized; pale with dark ocellar rings, sutures; dusky to dark frons, pronotal margin, midline and rugosities, basal and apical antennal segments, median and brief lateral longitudinal abdominal stripes, tarsal apices, thoracic sclera; dark recurrent scutoscutellar suture bisected by dark

line. Head with compound eyes set near posterior corners and occiput tapering abruptly posteriorly; mandibles without numerous, sclerotized teeth but terminating in 2 small lightly sclerotized teeth and penultimate membranous knob. Pronotum rectangular; corners rounded; width equaling head width; lateral margins narrow. Wings hyaline with forewing A2 branched; folded hindwing anal area with 3 veins; Rs of fore- and hindwing branched beyond cord; macropterous. Mesosternal Y-ridge unmodified. Terminal abdominal segments with evenly spaced long setae on lateral margins, lacking brushes of multiple hairs; hammer absent; abdominal pleural folds absent beyond segment 2. Cerci 7 or 8 segments; modified as per sex. (Figs. 7, 18; *see also* 14, 19)

Male

Tergum 9 produced into wide, posteriorly directed flap covering short, almost dorsally set segment 10, and into anteriorly projecting noselike hook extending to posterior tergum 8; hemiterga 10 modified posteriorly into thick, blunt, medially directed processes; transverse bands sclerotized, thick. Epiproct partially moderately sclerotized, hidden beneath hemitergal processes; anal lobe small. Epiproct tip not hinged, not recurved, membranous, hirsute, flat button; cowl not enlarged. Basal bar, anchor and reduced paragenital plates merged to form starlike, flat basal plate. Aedeagus tubular, membranous with 2 medial patches of dark spinulae anteriorly. Cerci modified basally; segment 1 elongate, convexly bowed, with paraproct as small, inwardly directed, pointed process basally; successive 3 segments compacted, fused; remainder of cercus unmodified with inconspicuous, thick, inward-pointing hair apically on each segment. (Figs. 99–102, 107, 108)

Female

Sternite 9 slightly concave, sparsely setose. Subgenital plate with semicircular posterior margin, flat to nearly concave ventrally, covering genital pore and overlapping most of sternite 9; arising medially on sternum 8 (especially obvious in lateral aspect) and separated from it by 2 longitudinal creases; base of plate accentuated by large indentations, particularly at terminations of posterior segmental fringe; posterior margin of plate bearing long, scattered hairs. Vagina membranous. Cerci slightly modified basally; segment 1 elongated; re-

mainder of cercus similar to *Suwallia* with inconspicuous but thick, inward-pointing hair apically on each segment. (Figs. 104–106)

Larva

To 10 mm. Presently not adequately distinguishable from *Suwallia*. (Figs. 29, 49; *see also* 34, 41, 98)

Ovum

Ovoid, swollen at equator yielding diamond profile; circular cross section; brown. Collar present, covering anterior pole, stalked, heavily incised and flanged, forming ruffled ring. (Fig. 62; *see also* 60, 61)

DISTRIBUTION AND SPECIES LIST: *Neaviperla* Ricker

Western Nearctic, probably eastern Palearctic.

forcipata (Neave) 1929, northern Rocky Mts.

MATERIAL EXAMINED

Neaviperla forcipata—ALASKA: Anchorage; Cold Bay; Kenai Pen.; Mt. McKinley Natl. Pk.; Paxson; Seward Pen.; Thomas Bay; Tiekel R. ALBERTA: Banff Natl. Pk. BRITISH COLUMBIA: Bowron L. Prov. Pk.; Garibaldi; Hazelton; Kisgegas; Owikeno L.; Vedder Crossing. MONTANA: Glacier Natl. Pk.

DISCUSSION

Neaviperla is closely related to *Suwallia* and very similar to it except for additional reproductive accessories. Males bear dramatically modified cerci and processes on tergum 9 (Figs. 99–102). Obscurity of tergum 10 and reduction of the epiproct and hemitergal processes indicate that part of their function in copulation may have been supplanted by modifications in cerci and terga. Females can be readily distinguished from *Suwallia* by elongate basal cercal segments (Fig. 106) and W thoracic suture marks (Figs. 6, 7).

Koponen and Brinck (1949) illustrated a male *Neaviperla* but labeled it as *Peltoperla*, a confusion due to the similar modifications of cerci in the two genera. The specimen, now lost, had no data on collection locality with it, but had been with some other material collected in Siberia. Zwick (1973) corrected the error in identification and extended the possibility that *Neaviperla* may occur in Asia.

Chloroperlini New Tribe

Epiproct tip an unhinged, recurved tab; basal bar and anchor completely merged, parallel-sided; paragenital plates reduced or absent; anal lobe prominent. Hemiterga of segment 10 unmodified. Aedeagus tubular, spinulated or supported by skeletal rods. Vagina thickened, spinulated. Adult mandibles normally dentate.

Chloroperlini includes the genera *Chloroperla* Newman 1836 (sensu stricto), *Haploperla* Navas 1934, *Isoptena* Enderlein 1909, *Plesioperla* Zwick 1967, *Pontoperla* Zwick 1967, *Plumiperla* new genus, *Rasvena* Ricker 1952, *Siphonoperla* Zwick 1967, *Triznaka* Ricker 1952, and *Xanthoperla* Zwick 1967. It occurs in the eastern and western Nearctic and the eastern and western Palearctic.

Triznaka Ricker

Alloperla (*Triznaka*) Ricker, 1952: 185. Type species: *Triznaka pintada* (Ricker).

Triznaka—Illies, 1966: 457.

DESCRIPTION

Adult

Body length 7 to 8 mm. Yellow to light fuscous, moderately to strongly sclerotized; generally pale with dark ocellar rings, medial and brief lateral abdominal stripes, recurrent scutoscutellar sutures and bisecting line, tarsal apices, basal and distal antennal segments, sutures, rugosities, wing veins; distinctly striped or patterned head and nota. Head with compound eyes set near posterior corners and occiput tapered abruptly posteriorly; mandibles with 4 or 5 sclerotized teeth. Pronotum rectangular; corners rounded; width equaling head width. Wings hyaline, with forewing A2 branched; folded

hindwing anal area with 3 veins; Rs of fore- and hindwing branched beyond cord; macropterous. Mesosternal Y-ridge unmodified. Terminal abdominal segments with evenly spaced long setae on lateral margins, lacking brushes of multiple hairs; hammer present on males, frequently on females, as minute, flat, eruption located medially on posterior margin sternum 7, flanked on each side by single long hair; abdominal pleural folds absent beyond segment 2. Cerci unmodified; 10–12 segments. (Figs. 8, 21; *see also* 14, 16)

Male

Tergum 9 medially indented on posterior margin; posterior half darkened, with bristly setae covering ⅔ width, medially interrupted by pale, setaeless keyhole-shaped area; hemiterga 10 unmodified, transverse bands sclerotized, thin. Epiproct non erectile, partially darkly sclerotized, nearly hidden between tergum and expanded sternum of segment 9; anal lobe enlarged, with posteriorly directed, scattered setae. Epiproct tip not hinged; anteriorly recurved, darkly sclerotized tab, as wide as, and nearly as long as, basal plate; tab, thick in lateral aspect, may be blunt, rounded, flat, ventrally minutely serrate; cowl not enlarged. Basal bar and anchor fused, forming flat, parallel-sided plate, twice as long as wide, anteriorly terminating at transverse bands, with scattered setae; paragenital plates reduced to faint dusky area at curve of epiproct tip, seldom obvious unless cleared, stained. Aedeagus tubular, membranous, with numerous thick rows of golden spinulae, patches of faintly iridescent spiny scales; terminating in thickened penis head. (Figs. 109–115)

Female

Sternite 9 slightly concave, sparsely setose. Subgenital plate rounded or flat on posterior margin; flat flap originating medially on sternum 8, overlapping most of sternum 9; lateral, but not anterior margins, indented from sternum 8 by membranous interruption; plate ¾ width of sternum. Vagina thickened, spinulated, visible through uncleared specimen. (Figs. 116–121)

Larva

To 8 mm. Tan to light fuscous, checkerboard appearance resulting from dusky and lighter patches on dorsum, particularly abdomen. Head with compound eyes set near posterior corners and occiput

abruptly tapered posteriorly. Maxilla terminating in single, large tooth, penultimate small tooth; dorsal aspect of paraglossa generally with single row of distinct, thick hairs on inner margin, scattered hairs on remainder of surface. Pronotum rectangular; corners rounded; width equaling, to slightly greater than, head width; fringe thick, even length, evenly spaced on circumference except for slight interruption on lateral margins. Wingpads convex on lateral margins, oblique on inner. Mesosternal Y-ridge unmodified. Clothing hairs thick, dark; posterior, bristle fringe of abdominal segments thick, even; long body hairs numerous, regular. Cerci with one each dorsal and ventral long fine hairs extending from posterior margin of each segment; these hairs as long as, to longer than, segment on posterior half of cerci; 14–17 segments. (Figs. 30, 42, 50, 122, 123; *see also* 34)

Ovum

Ovoid, circular cross section; light fuscous to brown. Collar present, stalked, incised, flanged. (*See also* Figs. 54–57 for similar ova)

DISTRIBUTION AND SPECIES LIST: *Triznaka* Ricker

Nearctic.

pintada (Ricker) 1952, western Nearctic.
signata (Banks) 1895, western Nearctic.

MATERIAL EXAMINED

Triznaka pintada—ARIZONA: Apache Co. CALIFORNIA: Sierra Co. COLORADO: Chaffee, Costilla, Eagle, El Paso, Grand, Gunnison, Huerfano, Jackson, Jefferson, Lake, La Plata, Park, Routt Cos. NEVADA: Elko, White Pine Cos. NEW MEXICO: Colfax, Rio Arriba, Sandoval, Santa Fe Cos. OREGON: Benton, Klamath Cos. SOUTH DAKOTA: Black Hills. UTAH: Duchesne, Juab, San Juan, Summit, Weber Cos. WASHINGTON: Whitman Co. WYOMING: Albany, Platte Cos.

T. signata—ALASKA: Delta Jct.; Glenn Hwy.; Matanuska Valley. ALBERTA: Lethbridge; Waterton Lakes Natl. Pk. BRITISH COLUMBIA: Chilcotin; Christina L.; Jackson; Prince George; Quesnel. COLORADO: Archuleta, Boulder, Chaffee, Eagle, Garfield, Grand, Gunnison, Hinsdale, La Plata, Larimer, Montezuma, Montrose, Park, Rio Blanco, Rio Grande, Saguache, Summit Cos. IDAHO: Bear Lake, Bonneville, Custer, Franklin, Latah, Lemhi, Valley Cos. MONTANA:

Big Horn, Carbon, Fergus, Flathead, Gallatin, Glacier, Golden Valley, Granite, Lake, Lincoln, Meagher, Missoula, Park, Ravalli, Stillwater, Sweet Grass, Wheatland Cos. NEW MEXICO: Colfax, Rio Arriba, Sandoval, San Miguel Cos. OREGON: Grant Co. SASKATCHEWAN: Broad Crk. UTAH: Beaver, Cache, Garfield, Morgan, Rich, Salt Lake, Sevier, Summit, Wasatch, Wayne Cos. WASHINGTON: Asotin Co. WYOMING: Albany, Fremont, Sheridan, Sublette, Teton, Uinta Cos.

DISCUSSION

Adults of *Triznaka* are readily distinguished from other Chloroperlinae by the distinct markings on head and pronotum (Figs. 3–12). A hammer is present only in *Triznaka* and *Rasvena* (Figs. 115, 150), but *Triznaka* lacks the aedeagal rods found in *Rasvena* (Figs. 112–114, 151). The blunt, thick epiproct tip (Figs. 111, 126), and absence of downy appendages on the aedeagus (Figs. 112, 127) serve to separate *Triznaka* from *Plumiperla*.

The anal lobe (Fig. 109) is proportionately smaller than in *Haploperla* (Fig. 137); and the W thoracic suture marks (Fig. 8) readily distinguish the species from similarly boldly patterned *Sweltsa*, with U thoracic suture marks (Fig. 4).

Larvae of *Triznaka* are also unique, with checkerboard patterning. They are the most thickly and regularly hirsute chloroperlid larvae. *Triznaka signata* (Fig. 123) bears an uninterrupted, light-colored longitudinal abdominal stripe; whereas *T. pintada* bears a beadlike abdominal stripe, alternating light and dark, checkerboard fashion (Fig. 122).

Triznaka is common in the Rocky Mountains. The genus even inhabits slower-flowing streams and creeks at lower elevations where other western Nearctic Chloroperlidae could not exist.

Plumiperla New Genus

Type species: *Triznaka diversa* (Frison) = *Plumiperla diversa* (Frison).

DESCRIPTION

Adult

Body length 6 to 8 mm. Light yellow, lightly to moderately sclerotized; pale with dark ocellar rings, medial and brief lateral abdominal stripes, recurrent scutoscutellar sutures and bisecting line, with dusky

pronotal margins, rugosities, tarsal apices, basal and distal antennal segments. Head with compound eyes set near posterior corners and occiput tapered abruptly posteriorly; mandibles with 4 or 5 sclerotized teeth. Pronotum rectangular, corners rounded, width equaling head width. Wings with forewing A2 branched; folded hindwing anal area with 3 veins; Rs of fore- and hindwing branched beyond cord; macropterous; hyaline. Mesosternal Y-ridge unmodified. Terminal abdominal segments with evenly spaced lateral margin of long hairs, lacking brushes of multiple hairs; hammer absent; abdominal pleural folds absent beyond segment 2. Cerci unmodified; 9–10 segments. (Figs. 9, 23; *see also* 14, 16)

Male

Tergum 9 medially, slightly indented on posterior margin, with bristly setae covering ⅔ width; hemiterga 10 unmodified, transverse bands sclerotized, thin. Epiproct non-erectile, partially darkly sclerotized, nearly hidden between tergum and expanded sternum of segment 9; anal lobe enlarged, with posteriorly directed, scattered setae. Epiproct tip not hinged, anteriorly recurved, darkly sclerotized tab, shorter in length than basal plate; tab, sharp in lateral aspect, may be pointed, rounded, generally narrower than basal plate; cowl not enlarged. Basal bar and anchor fused, forming flat, parallel-sided plate, twice as long as wide, anteriorly terminating at transverse bands, with scattered setae; paragenital plates reduced to faint dusky area at curve of epiproct tip, seldom obvious unless cleared, stained. Aedeagus tubular, membranous with rows, patches of golden spinulae, colorless or faintly iridescent spiny scales; terminating in thickened penis head plus pair of wispy, distally feathered appendages. (Figs. 124–129)

Female

Sternite 9 slightly concave, sparsely setose. Subgenital plate rounded on posterior margin; flat flap appearing as extension of sternum 8, overlapping sternum 9; base of flap ¾ width of sternum. Vagina thickened, spinulated, visible through uncleared specimen. (Figs. 130–135)

Larva

To 8 mm. Tan to light fuscous, generally concolorous with some pale areas. Head with compound eyes set near posterior corners and

occiput abruptly tapered posteriorly. Maxilla terminating in single, large tooth, penultimate small tooth; dorsal aspect of paraglossa generally with single row of distinct, thick hairs on inner margin, scattered hairs on remainder of surface. Pronotum rectangular; corners rounded; width equaling, to slightly greater than, head width; fringe thick, regular, except for lateral margins. Wingpads convex on lateral margins, nearly parallel to somewhat oblique on inner margins. Mesosternal Y-ridge unmodified. Clothing hairs not as thick or as dark as in *Triznaka*. Cerci with 2 to a few dorsal and ventral long fine hairs extending from posterior margin of each segment; these hairs as long as, to slightly longer than, segment on posterior third of cerci; 12–13 segments. (Figs. 31, 43, 51, 136; *see also* 34)

Ovum

Ovoid, circular cross section; fuscous to brown; chorion punctate. Collar stalked, incised, flanged. (*See* Figs. 54–57 for similar ova)

DISTRIBUTION AND SPECIES LIST: *Plumiperla* New Genus

Nearctic, eastern Palearctic.

diversa (Frison) 1935a, western Nearctic, northeastern Asia.
spinosa (Surdick) 1981, California.

MATERIAL EXAMINED

Plumiperla diversa—ALASKA: Anaktuvuk Pass; Anchorage; Fairbanks; Kenai Pen.; Mt. McKinley Natl. Pk.; Steese Hwy. ALBERTA: Banff Natl. Pk. BRITISH COLUMBIA: Kelvelet; Kootenay Natl. Pk.; Lillooet; Pine Valley; Quesnel; Saithers; Sumas R.; Terrace; Tetsa R.; Trout R.; Vancouver Isl.; Vedder Crossing; Williams L. CALIFORNIA: Los Angeles, Sierra Cos.; Lassen Volcanic, Yosemite Natl. Pks. COLORADO: Boulder, Clear Creek, Grand, Pitkin, Summit Cos.; Rocky Mt. Natl. Pk. IDAHO: Bear Lake, Blaine, Camas, Custer, Franklin, Fremont, Idaho, Lake, Lemhi Cos. MONTANA: Carbon, Deer Lodge, Flathead, Gallatin, Glacier, Granite, Lake, Lincoln, Meagher, Missoula, Park, Ravalli, Sweet Grass Cos. NEW MEXICO: Sante Fe, Taos Cos. OREGON: Hood River, Union, Wallowa Cos. UTAH: Cache, Davis, Duchesne, Grand, Morgan, Salt Lake, Sevier, Summit, Tooele, Utah Cos. WASHINGTON: Clallam, Jefferson, Kit-

titas, Pend Oreille, Pierce, Yakima Cos. WYOMING: Johnson Co. YUKON: White R.

P. spinosa—CALIFORNIA: Nevada, Sierra Cos.

ETYMOLOGY

The combination of the Latin term *plumi* with *perla* can be translated as "perla with down." It refers to the downlike appendages on the aedeagus.

DISCUSSION

Plumiperla differs from *Triznaka* in having a pointed profile of epiproct tip (Figs. 111, 126), feathered aedeagal appendages (Figs. 112, 127), and rounded female subgenital plate (Figs. 116, 117, 130, 131). It also differs from *Triznaka* in lacking a hammer and distinct patterning on adult and larva (Figs. 8, 9, 122, 123, 136). Females may be easily confused with *Suwallia* and *Alloperla*, but the W thoracic suture marks (Figs. 3, 6, 9) and spinulated vagina (Figs. 132–135) indicate *Plumiperla*.

Haploperla Navas

Haploperla Navas, 1934: 10. Type species: *Haploperla ussurica* Navas. (*Hastaperla* Ricker, 1935a; synonymized by Zwick 1977)

DESCRIPTION

Adult

Body length 5 to 7 mm. Pale yellow, delicately sclerotized; lacking dark or dusky markings except ocellar rings, distal half of antennae, apices of tarsi; may be dusky on pronotal margins, rugosities, median longitudinal abdominal stripe, sutures, recurrent scutoscutellar sutures and occasionally bisecting line. Head with compound eyes set near posterior corners and occiput tapering abruptly posteriorly; mandibles with 4 sclerotized teeth. Pronotum nearly square; corners rounded; width slightly narrower than head width. Wings hyaline with forewing A2 usually unbranched; anal area reduced, fold absent in fore- and hindwing; Rs of hindwing unbranched, of forewing sometimes branched beyond cord; macropterous. Mesosternal Y-ridge unmodified. Terminal abdominal segments with evenly spaced,

long setae on lateral margins, lacking brushes of multiple hairs; hammer absent; abdominal pleural folds absent beyond segment 2. Cerci unmodified; 7–9 segments. (Figs. 10, 20; *see also* 14, 16)

Male

Tergum 9 slightly produced medially posteriorly, with patch of short, stout bristles covering ⅔ width of distal half and medially interrupted by setaeless keyhole-shaped area; hemiterga 10 unmodified, transverse bands sclerotized, thin. Epiproct non-erectile, partially moderately sclerotized, nearly hidden between enlarged subgenital plate and tergum 9; anal lobe large, prominent, with numerous, scattered, long setae. Epiproct tip not hinged; anteriorly recurved, moderately sclerotized, minute chisel or tab as wide as, to twice as wide as, long; appearing as hooked protrusion of anal lobe or as distal edge of basal plate after it curls anteriorly beneath and against membranous anal lobe; semicircular shades of sclerotization visible dorsally, resulting from overlapping layers of basal plate and membrane as tip abuts anal lobe; cowl not enlarged. Basal bar and anchor fused, forming flat, parallel-sided, nearly square plate, terminating posterior to transverse bands; remnants of paragenital plates seldom visible at anal lobe base. Aedeagus tubular, membranous, with patches of various delicate, lightly sclerotized, faintly iridescent or colorless spinulae, scales; pair of delicate, thin, curved, lightly sclerotized skeletal rods, ¼ length of erigated organ, arising near distal end, directed over penis head. (Figs. 137–143)

Female

Sternite 9 not concave, usually sparsely setose. Subgenital plate appearing as posterior flaplike extension of sternum 8; margin of flat flap rounded or triangular, frequently barely overlapping sternum 9; base of plate often ¾ width of sternum, only slightly accentuated by break of segmental fringe and lateral creases; occasionally tapered posteriorly to concave-sided, triangle ¼ - ½ width of sternum. Vagina thickened, spinulated, visible through uncleared specimen. (Figs. 144, 145)

Larva

To 7 mm. Yellow to light tan, usually concolorous. Head with compound eyes set near posterior corners and occiput abruptly tapered

posteriorly. Maxilla terminating in single large tooth, penultimate small tooth; dorsal aspect of paraglossa with single row of distinct, thick hairs on inner margin, scattered hairs on remainder of surface. Pronotum nearly square, width slightly less than head width; fringe of hairs half as long as pronotum width, sparse, most numerous on anterior corners, most regular along posterior margin. Wingpads convex on lateral margins, nearly parallel on inner. Mesosternal Y-ridge unmodified. Clothing hairs sparse, pale; body hairs long, pale, scattered on wingpads, abdomen where longer than segment; long hairs tend to curve away from body instead of lie along it. Cerci with several fine long hairs extending obliquely posterior from posterior margin of each segment; these hairs 1½ times as long as segment on posterior ⅔ cerci; 12–13 segments. (Figs. 32, 44, 52, 146; *see also* 34)

Ovum

Nearly spherical; round cross section; light yellow to tan; chorion finely punctate. Collar present, not stalked; incised, flanged, frequently surrounded by large halo on ovum. (Figs. 58, 59)

DISTRIBUTION AND NEARCTIC SPECIES LIST: *Haploperla* Navas

Nearctic, 5 eastern Palearctic species.

brevis (Banks) 1895, eastern Nearctic, west to Alberta.
chilnualna (Ricker) 1952, British Columbia, south to California.
chukcho (Surdick and Stark) 1980, Mississippi.
orpha (Frison) 1937, northeastern Nearctic, west to Minnesota, Wisconsin.

MATERIAL EXAMINED

Haploperla brevis—ALABAMA: Calhoun Co. ALBERTA: Crawford; Drumheller; Edmonton; High Prairie; Valley View. ARKANSAS: Franklin, Garland, Hot Spring, Logan, Madison, Montgomery, Polk, Scott, Washington Cos. DELAWARE: New Castle Co. GEORGIA: Clarke, Forsyth Cos. ILLINOIS: La Salle, Union Cos. INDIANA: Parke Co. KENTUCKY: Rockcastle, Whitley Cos. MAINE: Washington Co.; Mt. Desert Isl. MANITOBA: Churchill; Duck Mt. Prov. Pk.; Pigeon R.; Swain R. MARYLAND: Allegany, Baltimore, Charles, Frederick, Washington Cos. MASSACHUSETTS: Hampshire Co. MICHIGAN: Crawford, Emmet, Grand Traverse, Hough-

ton, Iosco, Iron, Keweenaw, Lake, Marquette, Mason, Ogemaw, Ontonagon, Otsego Cos. MINNESOTA: Clearwater, Cook, Crow Wing, Hennepin, Hubbard, Lake, Pine, St. Louis, Stearns, Wadena Cos. MISSISSIPPI: Simpson Co. MISSOURI: Barry, Crawford, Greene, Iron, Madison, Taney Cos. NEW BRUNSWICK: Fredericton. NEW HAMPSHIRE: Coos, Grafton Cos. NEW YORK: Tompkins Co.; Adirondack Pk. NORTH CAROLINA: Guilford, Iredell, McDowell Cos.; Great Smoky Mts. Natl. Pk. NOVA SCOTIA: Moser R.; Parrsboro; Victoria. OHIO: Geauga, Hocking Cos. OKLAHOMA: Latimer, Le Flore, McCurtain, Pushmataha Cos. ONTARIO: Algonquin Pk.; Badeu; Batchawana; Charlton; Collingwood; Durham Co.; Kenora Dist.; Paudash L.; Singhampton; Terra Cotta. PENNSYLVANIA: Armstrong, Beaver, Chester, Luzerne, Northampton, Westmoreland Cos. QUEBEC: Gatineau Pk.; Great Whale R.; Lac Loup; Laurentides Prov. Pk.; Pk. Mt. Tremblant; R. aux Feuilles. SASKATCHEWAN: Hudsonia; Kennicott; Saskatchewan R.; Scudder. SOUTH CAROLINA: Oconee Co. TENNESSEE: Great Smoky Mts. Natl. Pk. VERMONT: Windsor Co. VIRGINIA: Augusta, Bath, Charlotte, Craig, Fauquier, Giles, Montgomery, Page, Prince William, Rockbridge, Rockingham, Shenandoah, Tazewell Cos.; Shenandoah Natl. Pk. WEST VIRGINIA: Hampshire, Hardy, Pendleton, Pocahontas, Preston, Randolph, Tucker Cos. WISCONSIN: Chippewa, Sawyer, Vilas Cos.

H. chilnualna—BRITISH COLUMBIA: Vancouver Isl. CALIFORNIA: Alpine, Los Angeles, Nevada, Placer, Riverside, San Bernardino, Sierra, Tulare Cos.; Yosemite Natl. Pk. OREGON: Benton, Douglas, Josephine, Lincoln Cos. WASHINGTON: Clallam, Jefferson, Mason, Pierce Cos.

H. chukcho—MISSISSIPPI: Claiborne Co.

H. orpha—MAINE: Washington Co. MINNESOTA: Anoka, Chisago, Crow Wing, Hennepin, Koochiching, Pine, St. Louis, Sherburne Cos. NEW BRUNSWICK: Fredericton. ONTARIO: Kenora Dist. QUEBEC: Montreal. WISCONSIN: Washburn Co.

DISCUSSION

Nearctic *Haploperla* adults are easily distinguished by small, delicate habitus (Fig. 10), wing venation (Fig. 20), wedge-shaped epiproct tip and large anal lobe (Figs. 137–139). Males do not bear as developed an epiproct tip or a hammer as do males of *Rasvena* (Figs. 147–150).

The genus also differs from other Nearctic and closely related Palearctic forms in the width and shape of the skeletal rods (Figs. 140–143).

Haploperla larvae are easily distinguished by delicate habitus, pale color, long, oblique setae, and parallel inner margins of wingpads (Figs. 32, 52, 146). Other Chloroperlidae genera, except *Rasvena*, are not as delicate, have shorter setae, and oblique inner margins of the wingpads. The lack of distinct color pattern in *Haploperla* (Fig. 146) differentiates the larvae from *Rasvena* larvae (Fig. 154).

Haploperla species are generally common and are more tolerant of slow, lowland streams than most other chloroperlids. They even inhabit some warm, silty streams of the Coastal Plain. Because of the survival ability and subsequent increased vagility of the genus, *Haploperla* has been able to invade much of the Nearctic. Subsequent isolation of populations has resulted in variability within some species.

Rasvena Ricker

Chloroperla (*Rasvena*) Ricker, 1952: 189. Type species: *Rasvena terna* (Frison).

Rasvena—Illies, 1966: 448.

DESCRIPTION

Adult

Body length 4 to 5 mm. Light yellow, delicately sclerotized; dark ocellar rings; dark to dusky median and brief lateral abdominal stripes, pronotal margins, sutures, recurrent scutoscutellar suture and bisecting line, distal segments of antennae, tarsal apices, cercal apices, venter. Head with compound eyes set near posterior corners and occiput tapering abruptly posteriorly; mandibles with 4 or 5 sclerotized teeth. Pronotum oval; width less than head width. Wings hyaline with forewing A2 usually branched; reduced but folded anal areas; Rs of fore- and hindwing branched beyond cord; macropterous. Mesosternal Y-ridge unmodified. Terminal abdominal segments with evenly spaced long setae on lateral margins, lacking brushes of multiple hairs; hammer present as per sex; abdominal pleural folds lacking beyond segment 2. Cerci unmodified; 7–9 segments. (Figs. 11, 22; *see also* 14, 16)

Male

Tergum 9 slightly produced medially posteriorly, with patch of slightly shorter, stouter bristles covering ⅓ width of distal half and medially interrupted by setaeless keyhole-like area; hemiterga 10 unmodified, transverse bands sclerotized, thin; hammer present as minute, flat eruption located medially on posterior margin of sternum 7. Epiproct non-erectile, partially heavily sclerotized, nearly hidden between enlarged subgenital plate and tergum 9; anal lobe large, prominent, with numerous, scattered, long setae. Epiproct tip not hinged; anteriorly recurved, heavily sclerotized, minute thorn- or clawlike tab, as wide as long; cowl not enlarged. Basal bar and anchor fused, forming slightly concave, parallel-sided plate, twice as long as wide, terminating posterior to transverse bands; paragenital plates absent. Aedeagus tubular, membranous, with patches of delicate, colorless spinulae, scales; pair of delicate, thin, curved, lightly sclerotized skeletal rods, ¼ length of erigated organ, arising near distal end, directed over penis head. (Figs. 147–151)

Female

Sternite 9 not concave, sparsely setose; posterior margin with small, horizontal patch of pale spinulae. Subgenital plate appearing as posterior flaplike extension of sternum 8; flap subtriangular, partially overlapping sternum 9, with longer setae on posterior margin; base of plate hardly distinguishable from remainder of sternum. Vagina thickened, mostly membranous with 2 patches of spinulae. (Figs. 152, 153)

Larva

To 5 mm. Light yellow, dusky striped and mottled. Head with compound eyes set near posterior corners and occiput abruptly tapered posteriorly. Maxilla terminating in single large tooth, penultimate small tooth; dorsal aspect of paraglossa with single row of distinct, thick hairs on inner margin, scattered hairs on remainder of surface. Pronotum oval, width slightly less than head width; fringe of long hairs nearly complete, sparse laterally. Wingpads convex on lateral margins, nearly parallel, slightly oblique on inner margins. Mesosternal Y-ridge unmodified. Clothing hairs numerous, pale; body hairs numerous, pale. Cerci with one each to a few dorsal and ventral fine

long hairs extending posteriorly from posterior margin of each segment; these hairs 1½ times as long as segment on posterior half of cerci; 13–14 segments. (Figs. 33, 45, 53, 154; *see also* 34)

Ovum

Unknown.

DISTRIBUTION AND SPECIES LIST: *Rasvena* Ricker

Nearctic.

terna (Frison) 1942, eastern Nearctic.

MATERIAL EXAMINED

Rasvena Ricker: NEW YORK: Adirondack Pk. NORTH CAROLINA, TENNESSEE: Great Smoky Mts. Natl. Pk. VERMONT: Orange Co. WEST VIRGINIA: Pocahontas Co.

DISCUSSION

Rasvena adults most resemble *Haploperla* and *Plumiperla* in the delicate, pale habitus (Figs. 9, 10, 11) and in the superficial appearance of the epiproct (Figs. 126, 139, 149). Wing venation, however, clearly differentiates the genera (Figs. 20, 22, 23). *Rasvena*'s aedeagus (Fig. 151) lacks the downy appendages of *Plumiperla* (Fig. 127) and bears thicker skeletal rods than Nearctic *Haploperla* (Figs. 140–143).

Rasvena larvae (Fig. 154) are separable from *Triznaka* (Figs. 122, 123) and *Plumiperla* (Fig. 136) by their small size, delicate appearance and distinctive coloration. The larvae differ from *Haploperla* (Fig. 146) in the patterned dorsum and in increased hirsuteness. *Rasvena is* rarely collected, but may be locally common.

Chloroperla (sensu lato)

Chloroperla ovibovis Ricker, from northwestern Canada, was included in the genus *Triznaka* on the basis of similarities particularly with, then congeneric, *Plumiperla diversa* (Zwick 1967). Zwick (1972) again discussed *C. ovibovis*, indicating its close relationship to *Chloroperla longidentata* Rauser 1968, from Mongolia. He mentioned the problematical nature of *Triznaka* and included both species in the genus.

Triznaka was indeed polyphyletic, and included two monophyletic genera, *Triznaka* sensu stricto and *Plumiperla* new genus, plus two *Chloroperla* sensu lato species. *Chloroperla ovibovis* and *C. longidentata* are distinct from *Triznaka* and *Plumiperla* because of the presence of skeletal rods and the absence of downy filaments on the aedeagus (Rauser 1968). The two species may be closely related, as evidenced by the similarity of characters, and their affinities with other Chloroperlinae are under investigation. The shape of the skeletal rods, however, indicates that probably neither one is *Chloroperla* sensu Zwick (1967).

Chloroperla (s.l.) *ovibovis* Ricker 1965

DESCRIPTION

Adult

Body length 5 to 6 mm. Pale yellow, delicately sclerotized; dusky to dark pronotal margin, midline, sutures, recurrent scutoscutellar suture and bisecting line, median and brief lateral abdominal stripes, antennal, tarsal, cercal apices. Head with compound eyes set near posterior corners and occiput tapered abruptly posteriorly. Pronotum oval, width less than head width. Wings hyaline with forewing A2 usually unbranched; anal area reduced in forewing, slightly reduced, folded in hindwing; Rs of fore- and hindwing branched beyond cord; macropterous. Mesosternal Y-ridge unmodified. Terminal abdominal segments with evenly spaced, long setae on lateral margins, but without brushes of multiple hairs; hammer absent. Cerci unmodified. (Figs. 12, 24; *see also* 14, 16)

Male

Tergum 9 slightly produced medially posteriorly, as setaeless, dark flap; with patch of short, stout bristles covering ⅔ width of middle of tergum; both flap and bristles medially interrupted by setaeless keyhole-shaped area; anterior margin supported by thin transverse band. Hemiterga 10 unmodified, transverse bands sclerotized, thin. Epiproct non-erectile, partially darkly sclerotized; anal lobe enlarged. Epiproct tip not hinged; anteriorly recurved, darkly sclerotized tab, three times longer than wide and as long as basal plate; tab pointed in lateral aspect, a flat oval as wide as basal plate; cowl not enlarged.

Basal bar and anchor fused, forming flat, parallel-sided plate, three times longer than wide, split anteriorly at transverse bands; paragenital plates absent. Aedeagus tubular, membranous with patches of colorless spinulae, scales; pair of delicate, curved, lightly sclerotized skeletal rods, bluntly terminated with minute spinulae, arising near distal end, directed over penis head. (Figs. 155–158)

Female

Sternite 9 sparsely setose. Subgenital plate broadly rounded to blunt on posterior margin; flat flap originating medially on sternum 8, overlapping most of sternum 9; flap base ¾ width of sternum, lateral indentations evident at termination of posterior segmental fringe; plate bearing longer setae than remainder of sternum. (Figs. 159, 160)

Larva

Unknown.

Ovum

Unknown.

DISTRIBUTION: *Chloroperla* (s.l.) *ovibovis* Ricker 1965

Northwestern Nearctic.

MATERIAL EXAMINED:

ALASKA: Glennallen; Steese Hwy. NORTHWEST TERRITORY: MacKenzie; Muskox L.

DISCUSSION

Chloroperla ovibovis appears most similar to *Triznaka* and *Plumiperla* on the basis of epiproct tip (Figs. 111, 126, 157), basal plate, anal lobe (Figs. 109, 124, 155), and general appearance (Figs. 8, 9, 12). It lacks the downy aedeagal appendages of *Plumiperla* (Figs. 127–129), however, and bears the skeletal rods (Fig. 158) absent in *Triznaka* (Figs. 112–114). A tablike, rather than wedge- shaped, epiproct tip (Fig 157) readily distinguishes *Chloroperla ovibovis* from *Haploperla* (Fig. 139), and a distinctive tergum 9 (Figs. 155, 156) distinguishes it from *Rasvena* (Figs. 147, 148).

Chloroperla cydippe Newman 1839 Nomen Dubium

The original description of *Chloroperla cydippe* is too vague to permit a clear definition of the species. Since the name was published, it has frequently been used in connection with *Haploperla brevis* (Needham and Claassen 1925; Frison 1935b; Claassen 1931) and with *Haploperla chilnualna* (Hoppe 1938).

Ricker (1938) examined the two female cotypes and designated one the Hololectotype. His redescription and illustration of the female subgenital plate corroborate his opinion that *C. cydippe* is not any of the *Haploperla* species. Neither is the wing venation of *C. cydippe* reduced as in *Haploperla*, nor is the subgenital plate characteristic of the latter genus.

Illies (1966) designated *Chloroperla cydippe* a *nomen dubium* since it cannot be assigned to a definite taxon. Because of the confusion involved, should the types be identified, the name is best kept unused, until it can be applied correctly.

Phylogenetic Relationships

Recent, mainly cladistic, analyses by Illies (1965, 1966) and Zwick (1973, 1974) have clarified the possible position of the family Chloroperlidae in plecopteran phylogeny, and have served as the basis for its classification. Phylogenetic considerations of Nearctic genera have been limited (Ricker 1943, 1950), although discussions of Palearctic and Oriental faunas have been more extensive (Despax 1941; Rauser 1968; Zwick 1967, 1971, 1972, 1977). Except for Zwick's work, indications of relationship frequently have depended on few characters, generally restricted to external morphology of male genitalia.

Although a phylogenetic hypothesis is best proposed on the basis of all known relatives, this detailed investigation of Nearctic species has contributed information useful in modifying prior propositions. A phylogenetic tree (Fig. 161) illustrates proposed generic relationships based on both cladogenesis and anagenesis. In a cladistic analysis (Fig. 162), based on recency of common descent, monophyletic taxa are delimited by synapomorphic characters. Additional investigations of Palearctic Chloroperlini are necessary and are continuing in order to provide a better understanding of relationships within the tribe.

CHARACTERS USED IN CONSTRUCTING PHYLOGENY

Each number refers to a character couplet in Figure 162. The apomorphic state is labeled.

1. Epiproct tip hinged.

The plesiomorphic state is not hinged, although anterior recurving is likely. (*See* 3, below)

2. Basal bar thickened, set medially or posteriorly on tergite, with reduced supportive structures.

In the plesiomorphic state, the basal bar is elongated, thin, curved, and attached to the basal anchor situated anteriorly on segment 10. The paragenital plates are thick and parallel to the basal bar. (*See* 3, below)

3. Basal anchor enlarged.

The ancestral state of the epiproct is similar to that of Paraperlinae, Pteronarcyidae, and primitive Perlodidae. The basal anchor anchors the epiproct at the anterior of tergum 10, and, with additional support from the paragenital plates, enables the basal bar to act as a lever, elevating the epiproct tip out of the deep cleft. With diversification of reproductive behavior, possibly accompanied by changes in erectibility of the epiproct tip, and spinulation and function of the aedeagus, the epiproct provided a slightly altered function. A hinged epiproct tip may require enlarged basal anchor and paragenital plates for support. A nonhinged epiproct, set in a shallow cleft, may require less elevation of the epiproct tip and modifications in support structures such as a reduced basal anchor, a thickened basal bar, and rearranged paragenital plates.

The epiproct tip is apparently useful in hooking open the female subgenital plate in order to expose the genital opening during copulation. In some species, the epiproct tip may be reduced to an extent that it is no longer used for that purpose. The hemitergal processes of *Suwallia* and tergal process of *Neaviperla* may have adopted part of the function of the epiproct tip.

4. Aedeagus spinulated.

Although representatives of both *Sweltsa* and *Bisancora* have developed a lightly sclerotized aedeagal plate, the tribes Suwalliini and Chloroperlini characteristically bear uniquely specific patterns of spines or scales on the aedeagus. The ancestral aedeagus is believed to be membranous.

Modifications of both internal and external genitalia accompany behavioral changes and probably facilitate specific recognition. In Alloperlini studied, external deposition of sperm requires no aedeagal spinulae to position the aedeagus within the vagina. In Suwalliini and Chloroperlini, internal placement of an elaborate aedeagus during copulation may promote increased efficiency of sperm transfer. Note

that the individual's increased vulnerability to predators, because of awkwardness and duration of intimate coupling, is not necessarily more of a disadvantge than in external sperm deposition. Behavioral antics of mating can preoccupy individuals in either mating system discussed.

5. Lateral brushes present on posterior margins of male and female terminalia.

The plesiomorphic state may be characterized by evenly spaced long setae without brushes formed of multiple hairs. In Alloperlini, brushes may serve as sensory advancements over single setae for accurate synchronization and juxtaposition of abdomens during mating. In other tribes, internal spinulae or other setation may function similarly.

6. Hemitergal processes developed on male tergum 10.

In the plesiomorphic state, the hemiterga of segment 10 are not specialized for a particular function and are not produced into processes. (*See* 3, above)

7. Vagina thickened or spinulated.

The plesiomorphic vagina is believed to be membranous. The apomorphic state usually accompanies increased modification or spinulation of the aedeagus. (*See* 4, above)

8. Epiproct tip a membranous hairy knob or button.

The ancestral state is at least a sclerotized tab or projection.

Plecoptera often exhibit tendencies within lineages toward either increased or decreased complexity of the epiproct. In the relationship between Suwalliini and Chloroperlini, the uniquely reduced epiproct of Suwalliini is the derived character state. (*See* 3, above)

9. Paragenital plates, basal bar reduced.

In the plesiomorphic state, the basal bar and paragenital plates form a starlike support system. (*See* 3, above)

10. Stout bristles of varying prominence set posteriorly on male tergum 9.

The plesiomorphic state consists of unmodified setae and is shared with Alloperlini and Paraperlinae. Bristles may serve in tactile communication during mating.

11. Adult mandibles reduced.

Chloroperlini bear stoutly toothed, sclerotized mandibles, exhibiting the plesiomorphic state. In the apomorphic state, there is a reduction in number of teeth and prominence of adult mandibles, possibly accompanying changes in life history. For example, Suwalliini may not require adult feeding during maturation of ova because the ova are developed earlier in the life history. The acceleration may allow better synchronization with seasonal environmental factors and predation pressures. Several of the genera emerge late in the summer or in more northern latitudes, when the amount of time for reproduction is much less than for other Chloroperlinae, which emerge in spring and early summer or at more temperate latitudes. Ova that are more developed upon adult emergence promote earlier fertilization and deposition. Originally, perhaps, the genetic loss of mandible development in the pharate adult permitted an increase in the number or development of ova, by way of energy economics that was advantageous.

In contrast, the delay afforded the Chloroperlini for egg development may also allow the larva to invest all its energy in growth instead of egg production in the final instar, and may be associated with larval diapause and early emergence times.

The reduction of the adult mandibles in the Suwalliini may also be a form of specialization for a particular function.

12. Basal anchor consecutively double.

The plesiomorphic state is a single basal anchor.

13. Epiproct tip inflated.

The plesiomorphic state of the epiproct tip is flat or more two-dimensional, although curved. The apomorphic state is three-dimensional and often highly sculptured.

14. Y-ridge of mesosternum with median ridge extending nearly to mesosternacosta.

The plesiomorphic state, found in all Chloroperlinae except *Bisancora*, is merely a Y.

15. Pronotum expanded.

The ancestral state is believed to be squarely oval rather than narrowly flanged or broadly elliptical.

16. Tergal ridge developed on male.

In the plesiomorphic state, terga 8 and 9 are unmodified. Development of a tergal ridge may accompany increased size, sclerotization, and sculpturing of the epiproct tip.

17. Comb on larval maxillae.

A comb is absent in the plesiomorphic state. Found in no other Chloroperlinae, the comb may indicate food specialization by *Alloperla* larvae.

18. Epiproct enlarged, frequently with elaborately sculptured tip extending anteriorly over tergum 9.

In the plesiomorphic state, the epiproct tip extends anteriorly almost to tergum 9. (*See* 3, above)

19. Larval habitus streamlined, with paucity of setae.

This character reflects a specialization of habitat. *Alloperla* bears morphological adaptations for burrowing.

20. Cerci modified.

The basal cercal segments of both sexes and the male ninth tergum bear unique modifications in *Neaviperla.*

21. Hemiterga refined.

The hemitergal processes of *Suwallia* are long, and frequently the shape is unique for each species. In the plesiomorphic state, the processes of *Neaviperla* are shorter, blunter, and not as well developed.

22. Aedeagus with pair of filamentous appendages.

The plesiomorphic state has no such specialization.

23. Hammer present.

A hammer specialized for communication is absent in the plesiomorphic state.

Based on present data, further speculation on relationships within Chloroperlini has not been attempted. Generic affinities of Nearctic species must be ascertained through examination of the Palearctic fauna; then, both Nearctic and Palearctic genera must be compared.

Historical Biogeography

Seldom has the family Chloroperlidae been considered in discussions of historical biogeography of Nearctic Plecoptera. Stewart, *et al.* (1974) commented on the southwestern distribution of *Alloperla caudata* and *Haploperla brevis* into Oklahoma during the last glacial period. Ricker (1964) mentioned 20 species in a discussion of Canadian distributions. Ricker, *et al.* (1968) reported on Quebec stoneflies and their Appalachian elements, including six chloroperlines. Brinck (1958) reported on several species in Newfoundland and Labrador.

Although the potential for dispersal varies for each life stage, vagility in Chloroperlinae is low compared to most other organisms and many other Plecoptera. Like most other stoneflies, Chloroperlidae have been unable to colonize even long-established oceanic islands.

Compared to other flying insects, adult Chloroperlinae are weak fliers and vulnerable to desiccation. They are seldom found far from riparian vegetation. Dispersal of the individual probably results in up- and downstream progression, access to adjacent streams, and introduction to new watersheds. Females returning to the stream for egg deposition may be caught in the aquatic drift and swept downstream. Adults attracted to lights at night may have a better opportunity to invade new areas.

Larvae are also restricted by environmental requirements, and many burrowing forms are not available to aquatic drift, a highly potential dispersal mechanism, until later instars. But major floods, freshets, and underground movement to adjacent watersheds and springs may also be effective means of dispersal.

Ova, dropped into the water by females, are also liable to drift and flood, spreading downstream before settling and attaching to a substrate. Fertilized females, transported to new areas by flight, preda-

tors, or other means, may retain viable eggs even though the adult has died.

Correlations between present distribution, proposed phylogeny, and geographic changes enable speculations on the historical biogeography of Chloroperlinae. This hypothesis is necessarily general, especially because of insufficient data on Palearctic species. For example, increased collection and systematic study of Alloperlini will undoubtedly permit discovery of additional species and confirm generic affinities. Dispersal refers to taxon range expansion, is neither necessarily discernible nor separate from vicariance, and occurs relative to ecological constraints. Alternative possibilities are suggested where allowed by adequate data. Hypotheses of dispersal must be conservative, with the least assumptions of extinction, since extinction, although an essential aspect of evolutionary history, is difficult to ascertain.

Zwick (1973, 1974) suggested a common ancestor for Perlidae and Chloroperlidae, based on several synapomorphies. The oldest fossil record of Perlidae dates to the Cretaceous, but the origin of the family probably dates to the Permian (Stark and Gaufin 1976). If Chloroperlidae either shared an ancestor with or branched off Perlidae, its origin was possible from Permian until Oligocene, when all extant families are believed to have existed (Illies 1965).

Chloroperlidae are absent from the southern hemisphere. Conservative explanations indicate that either origin and dispersal occurred after separation of the continents during Cretaceous and early Cenozoic (Windley 1977), or the cool-adapted insects were unable to move southward across the equator.

The eastern Palearctic is here proposed as the location of chloroperlid origin. In addition to supporting most chloroperlid genera, the area provides a central region from which the genera could have eventually differentially dispersed. Paraperlinae branched early in chloroperlid evolution, possibly originating in the eastern Palearctic and dispersing via Beringia into North America. Genera and species of this subfamily are frequently extant in relict populations only.

The subfamily Chloroperlinae could have divided into the Alloperlini lineage and Chloroperlini (+ Suwalliini) lineage by early or middle Cenozoic when continents were in nearly modern configuration. In early Mesozoic, pre-Chloroperlinae or Chloroperlinae may have dispersed thoughout the Palearctic, particularly Europe, where

conditions permitted copious speciation. From Jurassic through Eocene, the Obik Sea, connected to the Tethys Sea via the Turgai Straits, formed a marine barrier effectively separating Europe and Asia (Müller 1974; Raven 1975). Thus the Palearctic Chloroperlinae were divided in two with the potential to develop separate lineages, Chloroperlini in Europe and Alloperlini in Asia. But a later evolution of the two lineages may instead have resulted from proto-Chloroperlini filtering through the Obik Sea–Turgai Straits barrier. Subsequent isolation from Asian relatives, rapid dispersal, and speciation could have established the lineage in Europe.

As the Obik Sea dried up in early Cenozoic (Müller 1974), Chloroperlini was able to reinvade Asia. The lineage may also have spread westward into the northeastern Nearctic when it adjoined Europe, prior to the Cenozoic (McKenna 1975; Raven and Axelrod 1974).

Alloperlini, evolving in the eastern Palearctic, spread throughout Asia, but never successfully invaded Europe. Japan has a number of endemic species from three mainland genera. The island probably had been successively open, via lowered sea level, to colonization by numerous invasions from the mainland.

Beginning in the Paleocene, especially during successive periods of low sea level, Beringia became an effective corridor for the dispersal of Chloroperlinae between Siberia and North America (Raven 1975; Hopkins 1967). Chains of mountain ranges in eastern Siberia remained practically unglaciated thoughout the Pleistocene and provided suitable routes for range expansion. Alloperlini could have used this route early and dispersed into North America.

Suwalliini is believed to share a common ancestor with Chloroperlini, but its origin is uncertain. An early origin in the Nearctic cannot be disregarded. Much of its history has been obscured by the modification of continents during glaciations.

The paucity of chloroperline species in northern Europe was largely influenced by Pleistocene glaciations. Cool-adapted or high altitude forms were prevented from escaping southward ahead of the glaciers or from postglacial northward expansion in suitable mountain streams (as accomplished by their Nearctic counterparts) because of the lack of north-south corridors in Europe.

The evidence of entry routes or origins of chloroperline genera in North America has been greatly obscured, and the history of the subfamily can be analyzed only as the net result of geographic and

climatic changes associated with Pleistocene events. During advancements of glaciers, average temperatures decreased and vegetational belts shifted southward. Unglaciated regions endured equally extreme ecological alterations (Ross 1965). Populations suffered extinction, or expanded their range southward with suitable climatic changes in advance of the glaciers, or survived in unglaciated refuges. Parts of northern Alaska, the driftless areas of Minnesota and Wisconsin, and unglaciated mountains, or nunataks, extending above the ice sheet, provided possible outposts for species during glacial advances. Interglacial periods witnessed a northward shift of ecological belts and repopulation of areas exposed by melting ice.

The last, most extensive glaciation, the Wisconsin, may have had the greatest influence on the present distribution of Chloroperlinae. It included three major ice sheets—Greenland, Cordilleran and Laurentide—with an ice-free corridor between the latter two (Matsch 1976; Flint 1971; Dott and Batten 1976) (Fig. 163). The corridor allowed dispersal during glacier retreats and remained open as a refuge during some glacier advances. Other major barriers to dispersal included Lake Agassiz, the Mississippi Embayment, Lake Bonneville, and the arid lowlands of drier climates (Ross 1965).

CHLOROPERLINI

The tribe Chloroperlini is presently distributed throughout both Palearctic and Nearctic Realms. Nonendemic Nearctic genera include *Haploperla*, with five species in Japan and eastern Russia, and *Triznaka*, with one Nearctic species also present in northeastern Russia. The 6 strictly Palearctic genera include 34 species. The minimal divergence in characters among species of *Haploperla* may indicate a comparatively recent history for the genus.

Ancestral Chloroperlini may have crossed from Europe, where a diverse fauna is extant, into the northeastern Nearctic when these continents were adjoined. The immigrants could have dispersed across the newly invaded region, ultimately become isolated from European counterparts, and given rise to the eastern *Rasvena*. However, the relationship of *Rasvena* to Palearctic Chloroperlini is unclear and further study may indicate that it is derived from an Asian ancestor that crossed Beringia. The single extant species remains a relict form in isolated populations. *Chloroperla ovibovis*, another relict species

whose affinities are unclear, appears to have descended from an eastern Palearctic ancestor and possibly endured Pleistocene changes in unglaciated northern refuges.

The distribution and number of extant *Haploperla* species in eastern North America appear to imply a dispersal route between Europe and North America. Nevertheless, the presence of several *Haploperla* species in the eastern Palearctic indicates that the genus probably entered the Nearctic by way of Beringia, and eventually dispersed between streams encompassed by the southern Canadian Shield and northern United States. In addition to encouraging vicariance, glacial advancements and associated climatic changes may have limited western dispersal but permitted the extensive eastern and southern dispersal of *Haploperla*.

The tolerance of *Haploperla* to a broader range of habitats than those withstood by other Chloroperlini may have assisted in the rapid spread of the genus. The Laurentide Ice Sheet and Lake Agassiz could have separated the eastern and western populations of the ancestral form, eventually promoting the two species groups, *H. chilnualna* and *H. brevis* (*H. brevis*, *H. orpha*, *H. chukcho*). After retreat of the last glaciers, *H. chilnualna* remigrated northward to its present distribution from British Columbia to California. The *H. brevis* group also moved northward into previously glaciated areas from Nova Scotia west to Minnesota and Alberta. Remnants of the genus remained in suitable southern localities and dispersal also occurred westward into Oklahoma. *Haploperla* may also have found refuge in both the driftless area of Wisconsin and the corridor between glacial ice sheets. Similar dispersal patterns have been suggested by Ross for *Allocapnia* (Capniidae; Plecoptera) (Ross and Yamamoto 1967; Ross, *et al.* 1967; Ross and Ricker 1971).

Present distribution patterns indicate that *Triznaka* and *Plumiperla* probably originated in the western Nearctic as descendents of early Asian chloroperlinids that crossed the Bering Strait. *Triznaka* dispersed northward after retreat of the Wisconsin Glaciation. More tolerant of warm, slow, silty streams than many other Chloroperlinae, it was able to remain in the southern Rocky Mountains. Eventually, the genus range was apparently interrupted, yielding a northern component, *T. signata*, and a southern component, *T. pintada*. Presently, both species ranges overlap; but *T. pintada* generally has more lowland distribution than *T. signata*. *Triznaka signata* has extended its

range into Alberta and British Columbia, while *T. pintada* has been recorded from southern California, where it may have spread from Arizona westward via the mountains. *Triznaka pintada* has also dispersed into the Black Hills of South Dakota where it remains isolated but morphologically identical to the parent population in the Rocky Mountains. Ross (1965) observed similar distributions for other eastern Cordilleran insects and proposed that dispersal occurred once, and recently, by way of cold-water stream connections between the Black Hills and the Bighorn Mountains. Disjunction may have also resulted from a recent vicariant event that severed the original range.

Populations of *Plumiperla* became isolated in the western and in the eastern Cordilleras, resulting in *P. spinosa* and *P. diversa*. *Plumiperla spinosa* may have evolved as a climatic relict in the mountains of southern California, while *P. diversa* moved northward in the Rocky and Cascade Mountains to Alaska. The genus has apparently invaded the Palearctic via Beringia with *P. diversa* recorded from Kamchatka (Zhiltzova and Zwick 1971; Levanidova and Zhiltzova 1979).

ALLOPERLINI

In addition to the Nearctic Realm, *Sweltsa* inhabits Assam and eastern Russia (5 species), and *Alloperla* inhabits Japan, Korea, Mongolia, Manchuria, Hindu Kush, Siberia, Kamchatka, and Kansu Province (20 species). *Sweltsa* and *Alloperla* may have originated in Asia, and probably entered North America separately, via Beringia. Both genera either spread across the continent, populating it differentially, or settled on part of the continent, with later expansions of range. In either case, *Sweltsa* was more successful in inhabiting the eastern and western Cordilleras, while *Alloperla* was more successful in the Appalachians. Separation of the genera and species pairs was promoted by the inhospitable midwest and Pleistocene glaciations. North-south and east-west species pairs within longitudinal mountain chains, clines, localized endemic species, and aberrant populations are represented in the tribe. There is also evidence of reinfiltration of previously glaciated areas from refuges and via corridors.

The progenitor of the *Alloperla severa* group (*A. severa*, *A. concolor*, *A. neglecta*, *A. delicata*, *A. medveda*, *A. serrata*) of species was probably divided into eastern and western constituents by Pleistocene glaciations. The eastern Nearctic component inhabited the cold, clear

streams of the higher Appalachian Mountains. Cooling temperatures accompanying glacial advances permitted the southward dissemination of *Alloperla* as far as the Great Smoky Mountains. Retreating glaciers and warming temperatures probably eliminated populations in lowland areas while a northern representative was able to extend its range northward into previously glaciated areas, engendering the species *A. concolor*. A remnant of the *A. severa* group was left in the high altitudes of the Smokies, becoming *A. neglecta*.

In the western Nearctic, the *A. severa* group spread southward into the eastern and western Cordilleras. Glacial advancement probably effectively isolated the two populations, and resulted in the formation of an *Alloperla delicata* form in the western Cordilleras and *A. severa* in the Rocky Mountains. After deglaciation both species remigrated north, where further isolating mechanisms severed the eastern extension of the *A delicata* form, giving rise to *A. medveda*. *Alloperla severa* diffused west and north into Oregon, Washington and Alaska. Its range was also sectioned into a northwestern and a southeastern population at a line running longitudinally through Montana and Idaho. The barrier involved may have been an uncrossable band of mountain glaciers separating the Mississippi and the Pacific drainage systems.

Alloperla caudata and *A. idei* form a north-south species pair as a result of Pleistocene events. *Alloperla idei* redistributed northward in a manner similar to *Haploperla orpha*, but exclusively east of the Great Lakes. *Alloperla caudata* eventually dispersed farther northward than *A. idei*, and retained a disjunct Ozark-Ouachita population, similar in distribution to *Haploperla brevis*.

Alloperla banksi, *A. imbecilla* and *A. hamata* share a common ancestor that dispersed as far south as Alabama during the cool periods of glacial advance. With the onset of a warmer climate, the precursor species displaced its range northward above the margin of glacial deposition (*A. banksi*), leaving behind relict populations in northern Alabama (*A. hamata)* and in the Ohio River drainage (*A. imbecilla*).

Alloperla vostoki and *A. voinae* are restricted to northeastern New England and eastern Canada. Refuge in unglaciated areas may have been possible, but are unlikely because of the silty nature of the streams that are believed to have existed there (Ross, Rotramel, Matrin, McAlpine, 1967). Both species probably share a common ances-

tor with more southerly distributed *Alloperla chloris*, and may have been isolated from it by a glacial lobe during the Pleistocene.

Two species groups descendant from a transboreal *Sweltsa* ancestor are represented in the eastern Nearctic. Nearest relatives of northeastern *Sweltsa naica* include the Cordilleran *S. coloradensis* (*S. coloradensis*, *S. pacifica*, *S. oregonensis*) species group. Its precursor probably became isolated in eastern Canada by the encroaching glaciers and may have survived in mountainous areas south of the glaciers. *Sweltsa naica* has reinvaded the previously glaciated northeast and has been found as relict populations as far south as West Virginia.

The second *Sweltsa* group is endemic to eastern North America and includes *Sweltsa lateralis*, *S. urticae*, *S. mediana*, and *S. onkos*. After Pleistocene glaciations, *S. lateralis* reinvaded the northern Appalachians with no apparent disjunctions of its range. *Sweltsa urticae* is limited to the southern Appalachian highlands. *Sweltsa mediana* and *S. onkos* represent another example of a north-south species pair, with the former restricted to the Great Smoky Mountains and southwestern Virginia, and the latter common in the northeastern Nearctic.

Southward dispersal of the western relatives of *Sweltsa naica* resulted in an isolated Rocky Mountain population that subsequently evolved into the unique *Sweltsa albertensis* group. The ancestral population of the group probably dispersed south during cooler, wetter times but, during a warm interglacial period, became bisected by a lowland barrier extending from southern Idaho to northern Colorado. The resultant isolation gave rise to the ancestors of *S. albertensis* in the northern Rockies and *S. lamba* in the central Rockies. During a later glacial period, the *S. albertensis* form probably again extended its range south as far as northern Utah. With warmer temperatures, *S. albertensis* redispersed northward, extended into Alberta and left a relict population south of the Snake River Plain that became *S. gaufini*. *Sweltsa lamba* has extended its range north into Idaho and west into Oregon, where it rarely overlaps the range of *S. albertensis*. Intervening lowlands have provided a reproductive barrier sufficient to result in morphologically divergent populations of *S. lamba*. In the Colorado Rockies, the epiproct tip of the male *S. lamba*, in dorsal aspect, terminates in a small angular projection proximal to the hooked apex. In Utah the same structure is thin and rounded, and in Oregon, it is widely rounded.

Sweltsa borealis, *S. fidelis*, and related species (*S. revelstoka*, *S. californica*, *S. continua*) in the eastern and western Cordilleras share a common ancestor from which none has diverged to the extent that they are always clearly distinguishable morphologically. Clinal variations of characters over distributional ranges are pronounced, and described species often represent regional extremes within broad species interpretations.

The genus *Bisancora* probably evolved in the western Cordillera from undetermined origin. A north-south species pair comprises the genus and apparently originated because of an arid barrier in the central Coast Ranges of California that effectively isolated the ancestral population.

SUWALLIINI

Suwallia is extant in both eastern and western Nearctic and in eastern Russia and Japan (8 species). *Neaviperla* is endemic to the northwestern Nearctic. Prior to Pleistocene glaciations or during an interglacial period a *Suwallia pallidula*-like ancestor probably dispersed throughout boreal North America. Eastern and western populations could have been separated by Canadian ice sheets. When Eastern *Suwallia* moved south into the Appalachian Mountains with ameliorating climate, it evolved into *S. marginata*. Divergence from the ancestral form has been minimal and, although extinctions may have occurred, there appears to have been little speciation in the eastern Nearctic.

In the western Nearctic, the ancestral form of *Suwallia pallidula* also moved south into both eastern and western Cordilleras. After glacial retreat, *S. pallidula* remigrated northward as far as Alaska. Throughout its range it exhibits regional and temporal variations that may result partially from Pleistocene occurrences. Similar influences effected the speciation of *S. lineosa* and *S. dubia*.

All species of *Suwallia* generally emerge later in the summer and autumn than most other Chloroperlinae. The temporal isolation associated with cold tolerance, and accompanied by an appropriately modified life history, undoubtedly resulted from or reinforced early evolution of the genus. Capacity for cold tolerance may have enabled the ancestors of *Suwallia autumna* and *Neaviperla forcipata* to sustain

existence in unglaciated but cold areas of Alaska. Both species have moved southward in their repopulation of previously glaciated areas. Further collecting in Siberia may reveal that *Neaviperla* has moved westward, as well.

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Figures

Fig. 1. *Sweltsa borealis* resting on *Mimulus guttatus*.

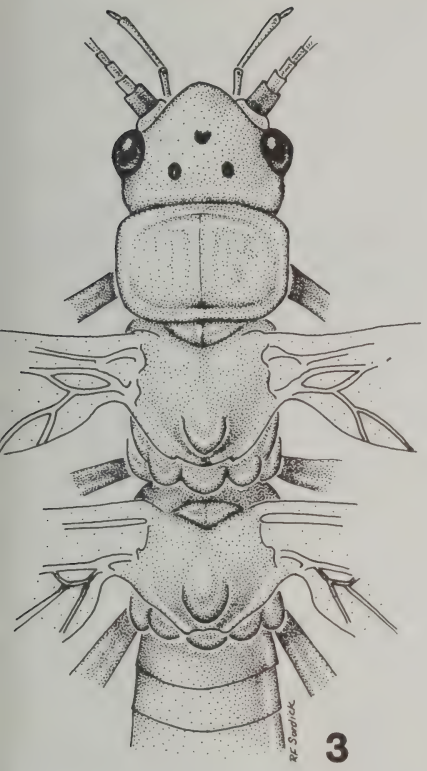


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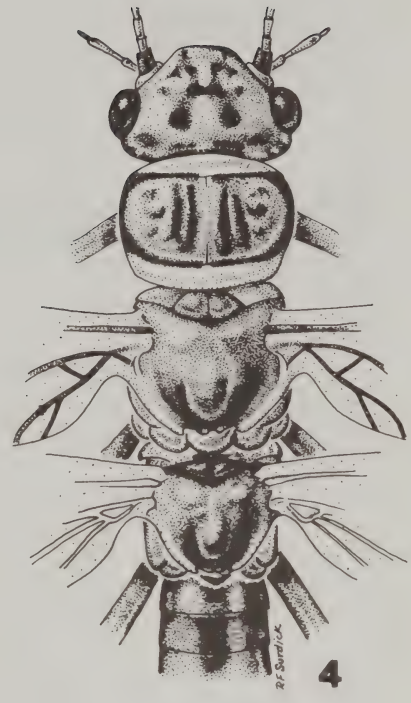
Fig. 2. *Sweltsa lateralis* ecdysing.



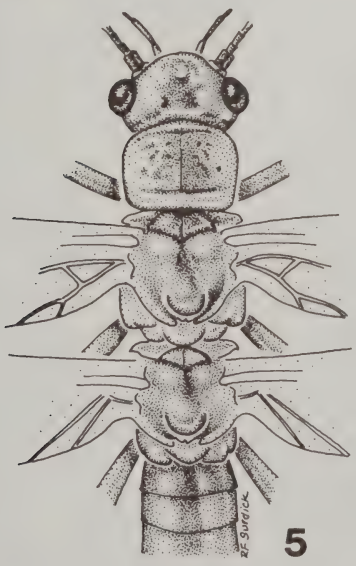
Figs. 3–5. Adult heads and nota: (3) *Alloperla severa*; (4) *Sweltsa coloradensis*; (5) *Bisancora rutriformis*.



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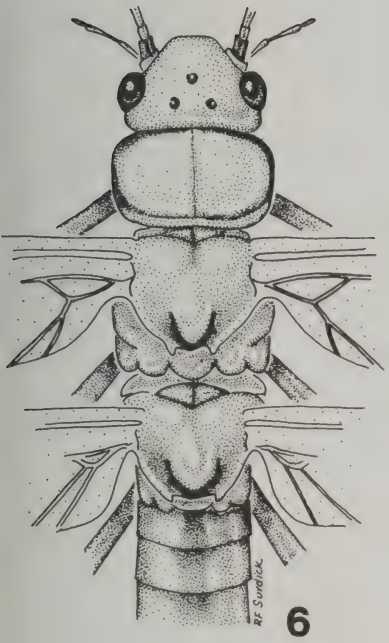


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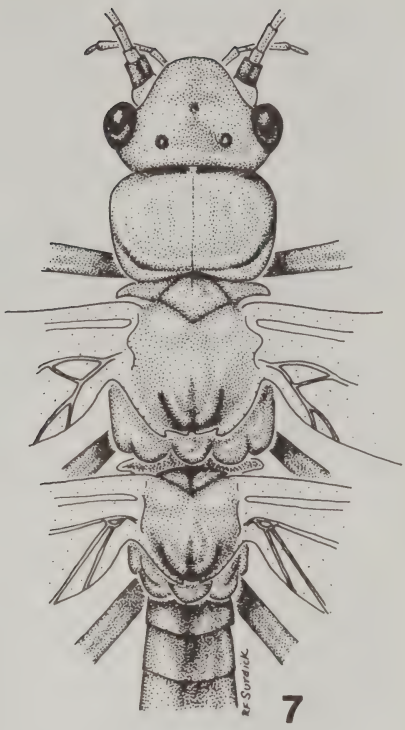


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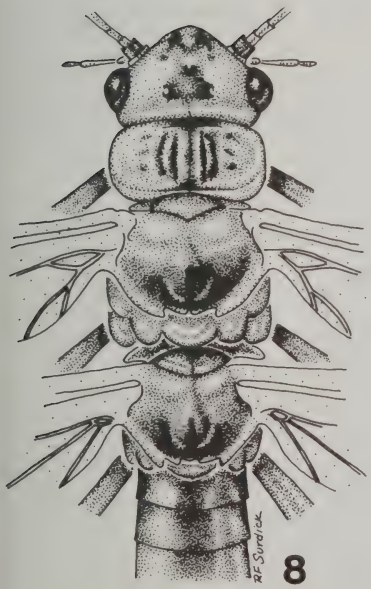
Figs. 6–9. Adult heads and nota: (6) *Suwallia pallidula*; (7) *Neaviperla forcipata*; (8) *Triznaka pintada*; (9) *Plumiperla diversa*.



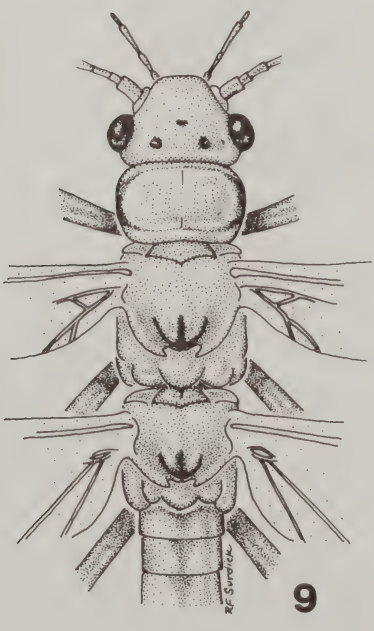
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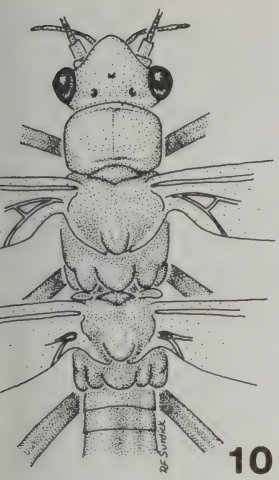


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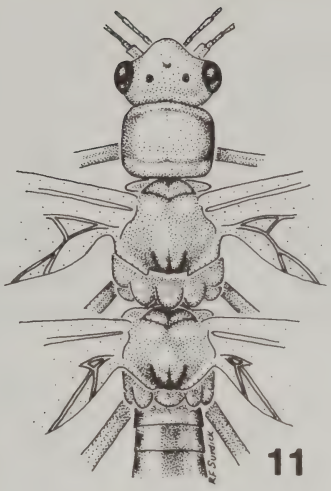


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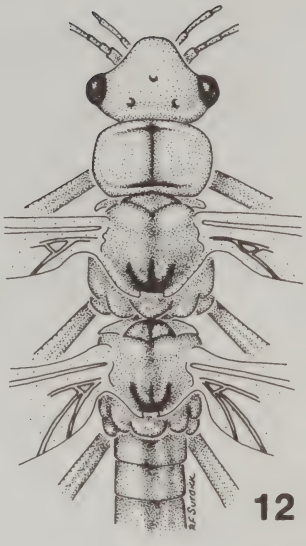
Figs. 10–18. Adult heads and nota: (10) *Haploperla brevis*; (11) *Rasvena terna*; (12) *Chloroperla* s.l. *ovibovis*. Male terminalia: (13) generalized features. Adult mesosternal Y-ridge: (14) *Alloperla severa*; (15) *Bisancora rutriformis*. Adult mandible: (16) *Alloperla severa*; (17) *Suwallia pallidula*; (18) *Neaviperla forcipata*.



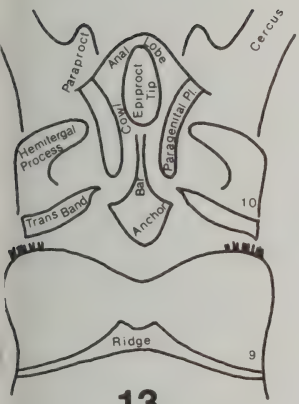
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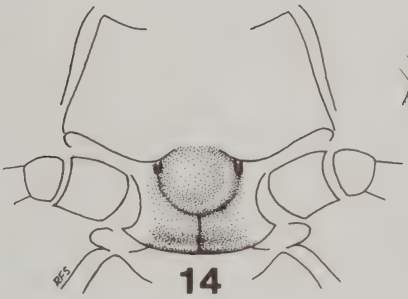
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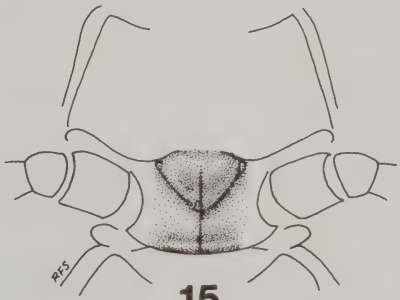
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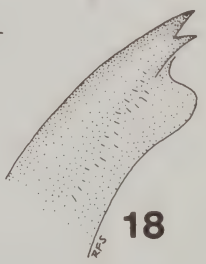
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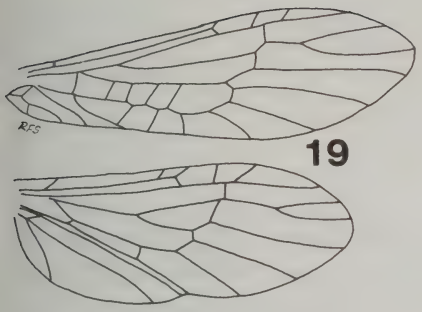


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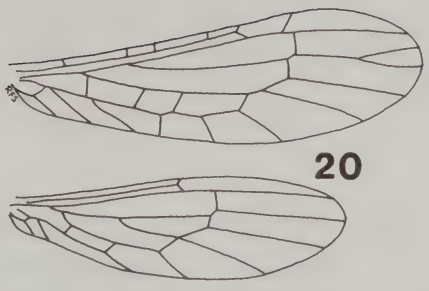


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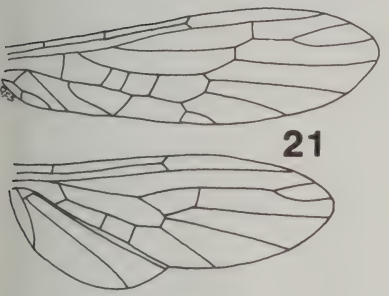
Figs. 19–25. Right wings (sizes not comparable): (19) *Sweltsa coloradensis*; (20) *Haploperla brevis*; (21) *Triznaka pintada*; (22) *Rasvena terna*; (23) *Plumiperla diversa*; (24) *Chloroperla* s.l. *ovibovis*; (25) *Sweltsa revelstoka*, brachypterous.



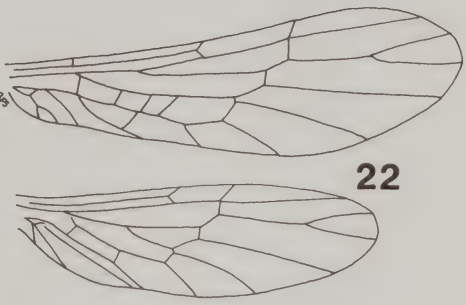
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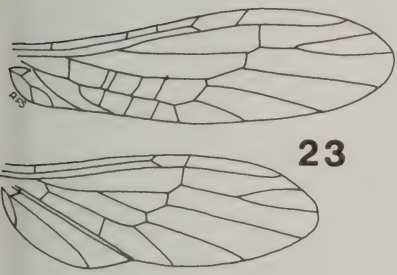
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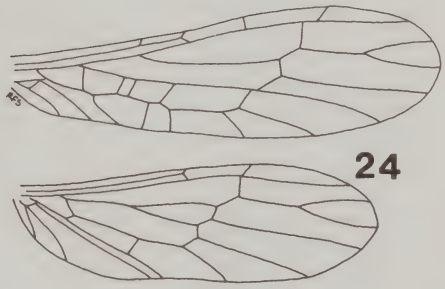
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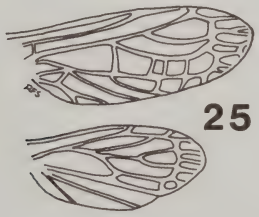
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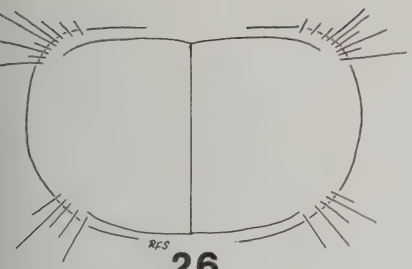


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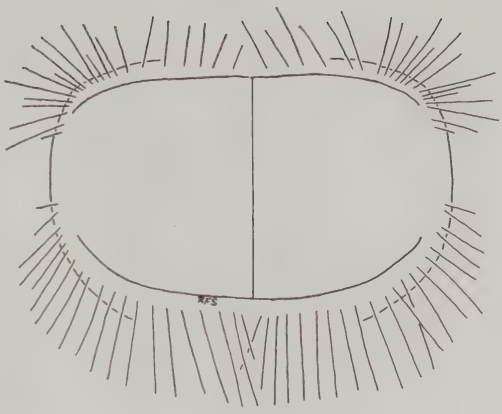


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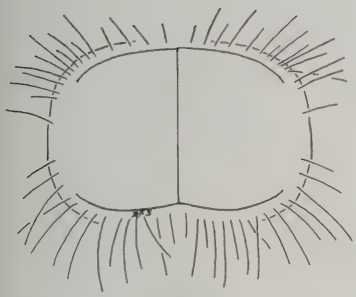
Figs. 26–33. Larval pronota: (26) *Alloperla severa*; (27) *Sweltsa coloradensis*; (28) *Suwallia pallidula*; (29) *Neaviperla forcipata*; (30) *Triznaka pintada*; (31) *Plumiperla diversa*; (32) *Haploperla brevis*; (33) *Rasvena terna*.



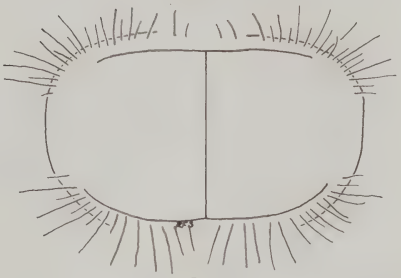
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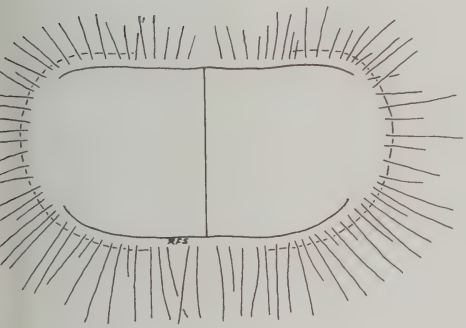
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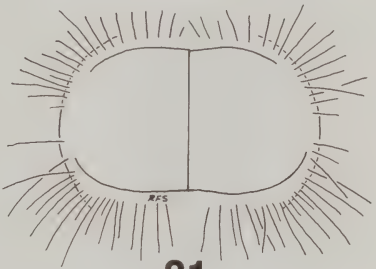
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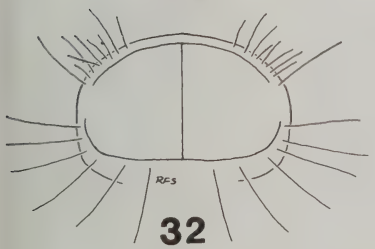
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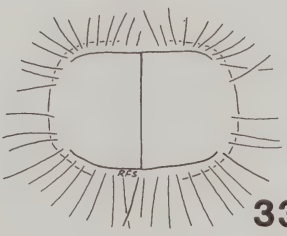
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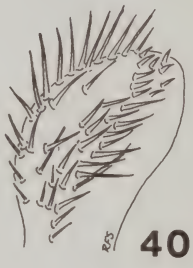
Figs. 34–45. Larval maxillae: (34) *Sweltsa coloradensis*; (35) *Alloperla severa*; (36) *Alloperla atlantica*. Larval mouthparts: (37) ventral; (38) paraglossae, dorsal. Larval paraglossae, dorsal: (39) *Alloperla severa*; (40) *Sweltsa coloradensis*; (41) *Suwallia lineosa*; (42) *Triznaka signata*; (43) *Plumiperla diversa*; (44) *Haploperla brevis*; (45) *Rasvena terna*.

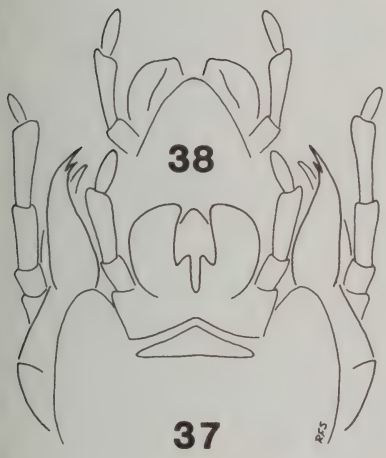

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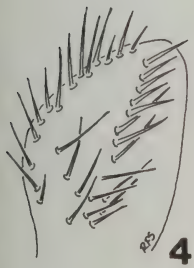

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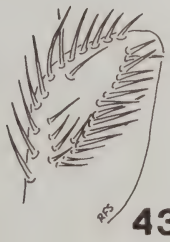

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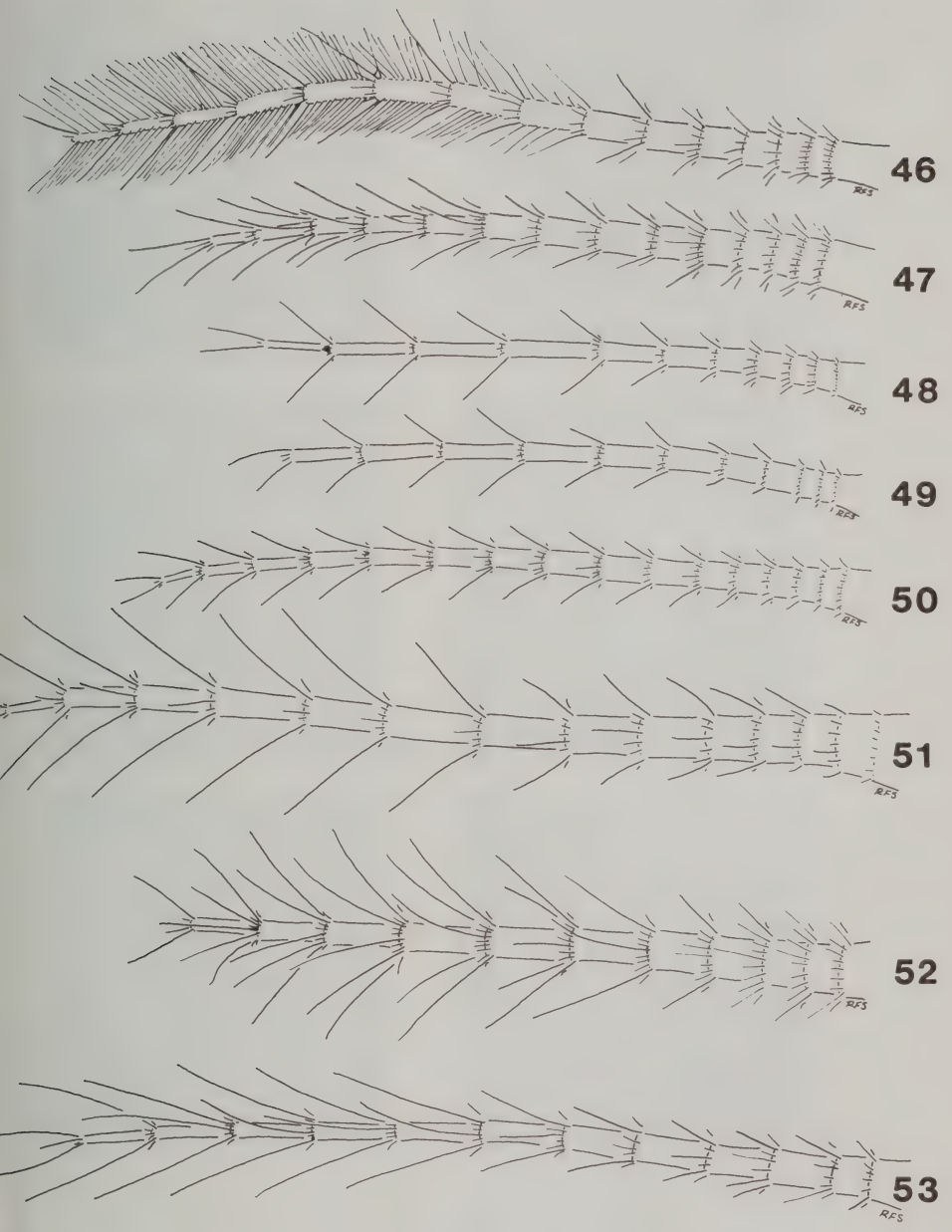

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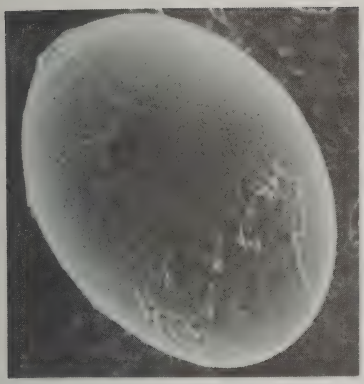

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Figs. 46–53. Larval cerci, lateral: (46) *Alloperla severa*; (47) *Sweltsa coloradensis*; (48) *Suwallia pallidula*; (49) *Neaviperla forcipata*; (50) *Triznaka pintada*; (51) *Plumiperla diversa*; (52) *Haploperla brevis*; (53) *Rasvena terna*.


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Figs. 54–59. Ova (Scanning electron micrographs): (54) *Alloperla caudata*, lateral; (55) *Alloperla caudata*, collar; (56) *Sweltsa coloradensis*, lateral; (57) *Sweltsa coloradensis*, collar; (58) *Haploperla brevis*, lateral; (59) *Haploperla brevis*, collar.



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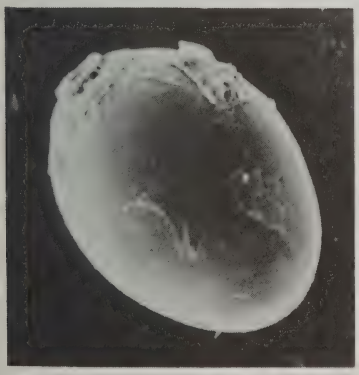
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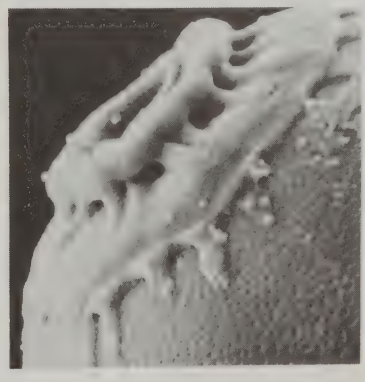
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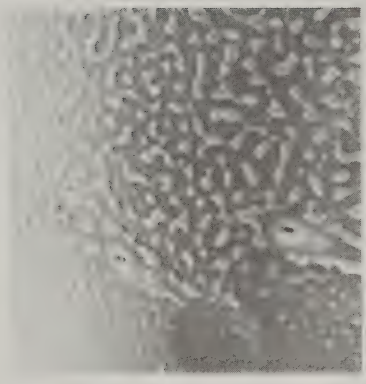


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Figs. 60–63. Ova (Scanning electron micrographs): (60) *Suwallia pallidula*, lateral; (61) *Suwallia pallidula*, micropyles; (62) *Neaviperla forcipata*, collar. *Sweltsa onkos*: (63) adult.



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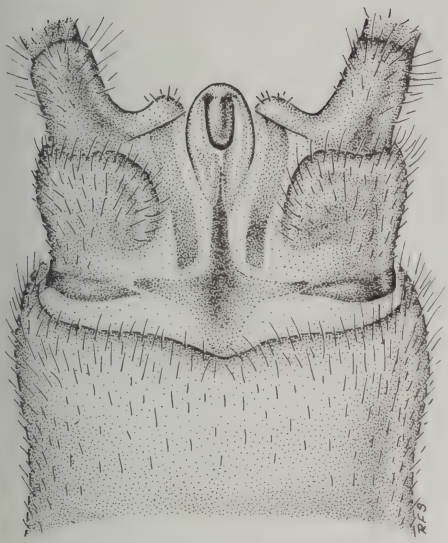


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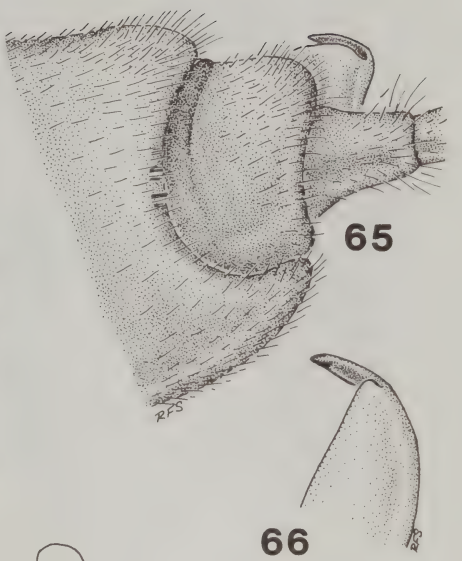


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Figs. 64–69. *Alloperla severa*: (64) male terminalia, dorsal; (65) male terminalia, lateral; (66) epiproct, elevated; (67) epiproct, dorsolateral; (68) aedeagus, dorsal; (69) aedeagus and terminalia, lateral.

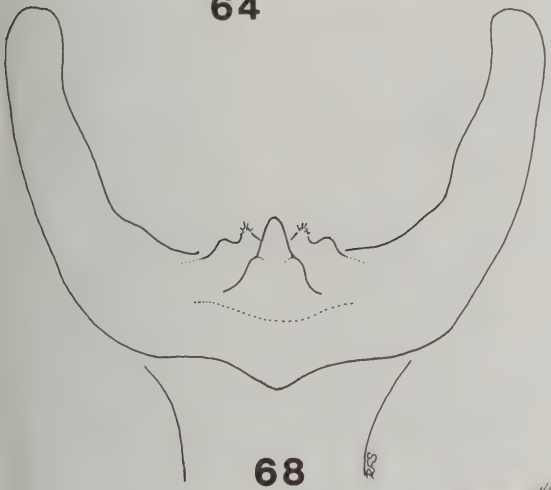


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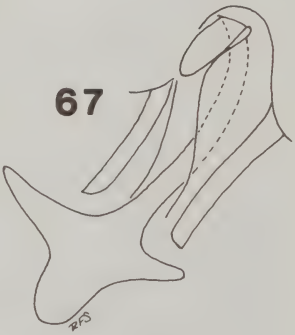


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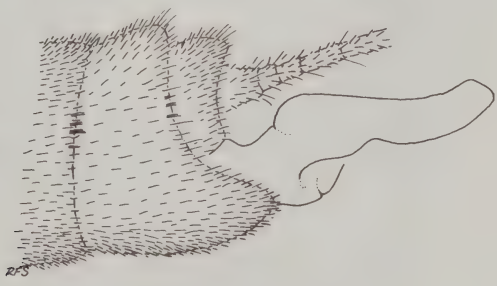
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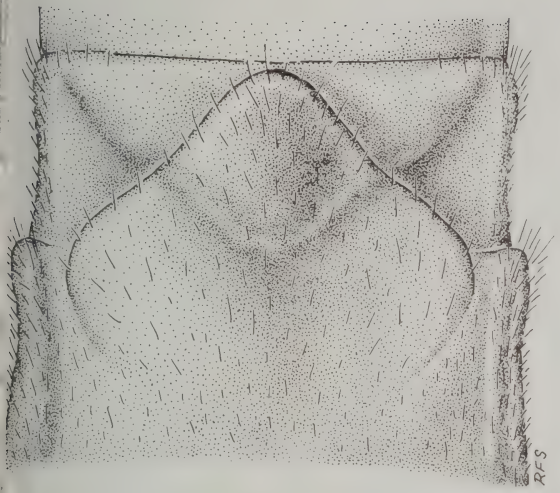


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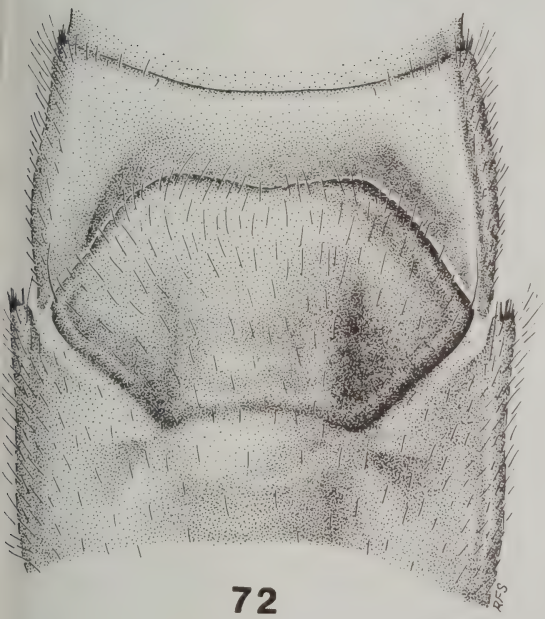
Figs. 70–73. *Alloperla severa*: (70) female terminalia, ventral; (71) female terminalia, lateral. *Sweltsa coloradensis*; (72) female terminalia, ventral; (73) female terminalia, lateral.



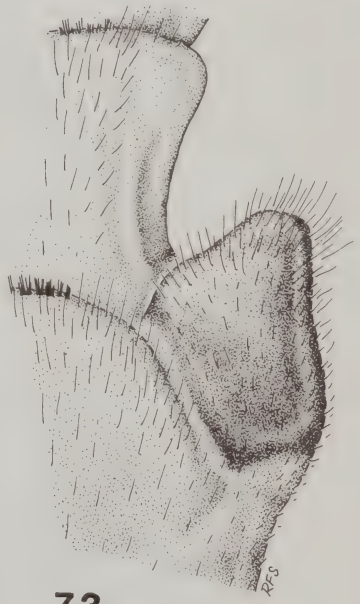
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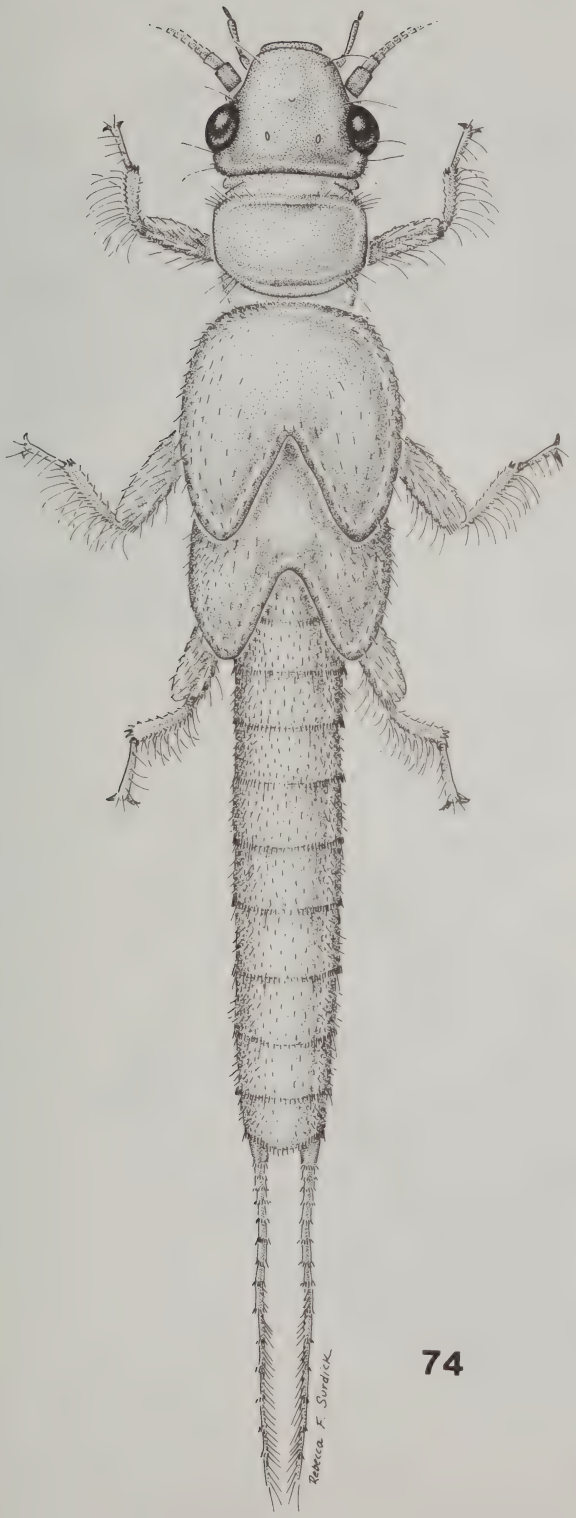


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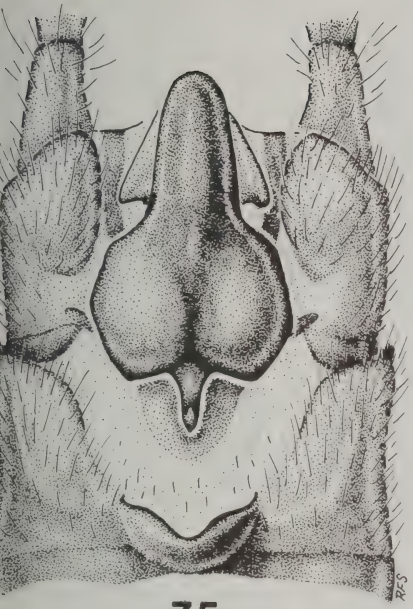
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Fig. 74. *Alloperla severa* larva.

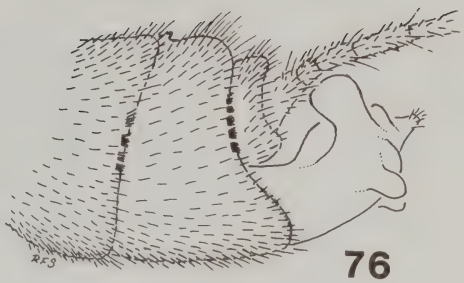


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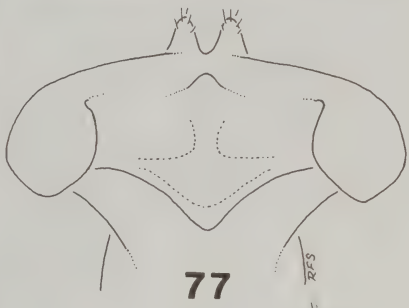
Figs. 75–80. *Sweltsa coloradensis*: (75) male terminalia, dorsal; (76) aedeagus and terminalia, lateral; (77) aedeagus, dorsal; (78) aedeagus, dorsolateral; (79) epiproct, dorsolateral; (80) male terminalia, lateral.



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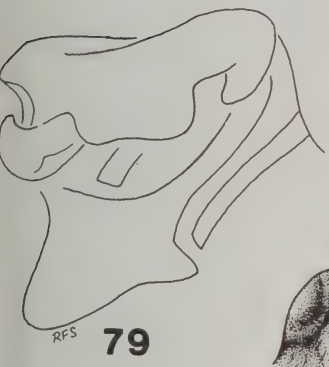
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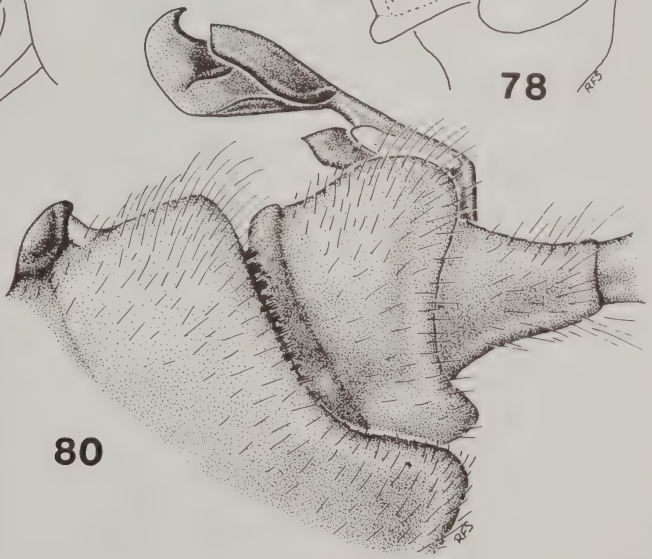
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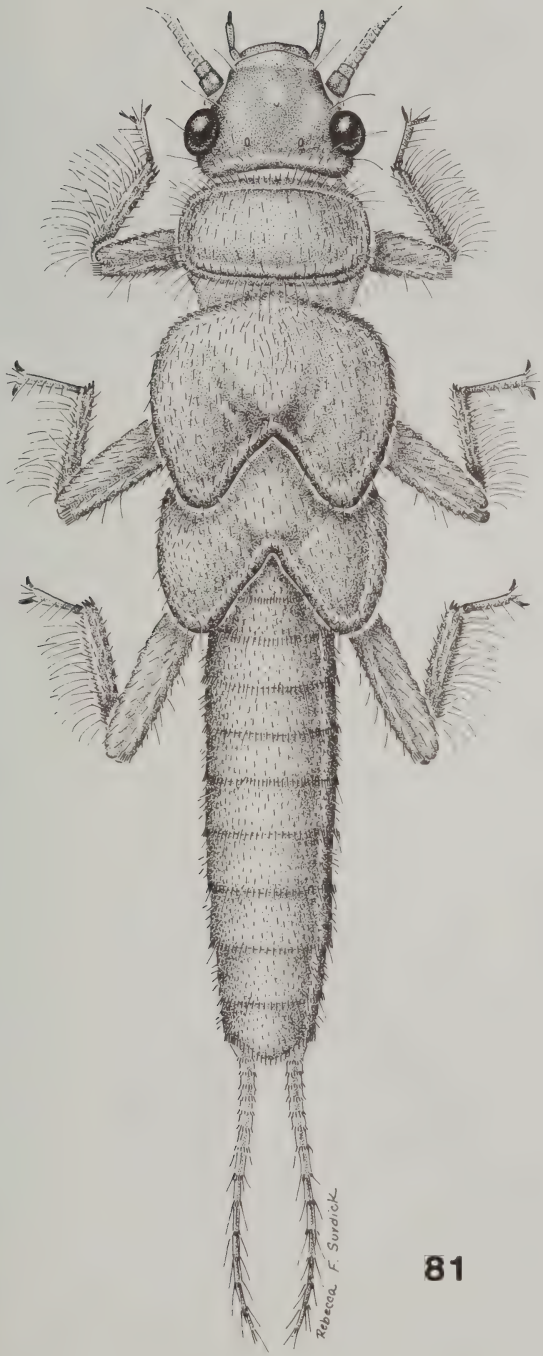


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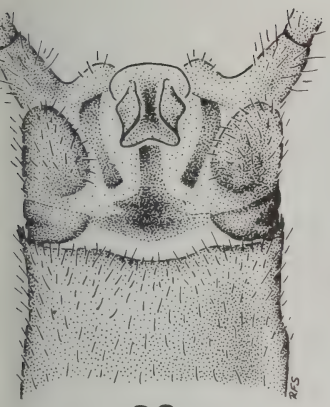
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Fig. 81. *Sweltsa coloradensis* larva.

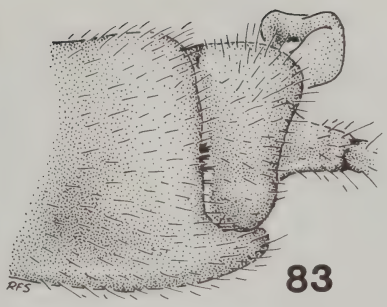


81

Figs. 82–90. *Bisancora rutriformis*: (82) male terminalia, dorsal; (83) male terminalia, lateral; (84) epiproct, elevated; (85) aedeagus, lateral; (86) aedeagus, dorsal; (87) aedeagus, ventral; (88) epiproct, dorsolateral; (89) female terminalia, ventral; (90) female terminalia, lateral.



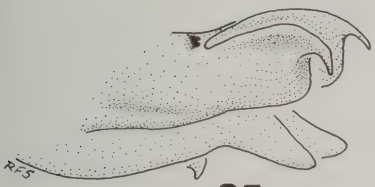
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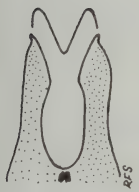
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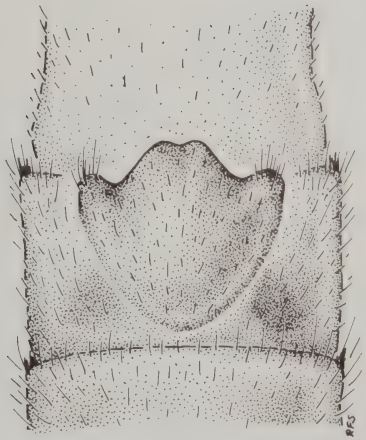
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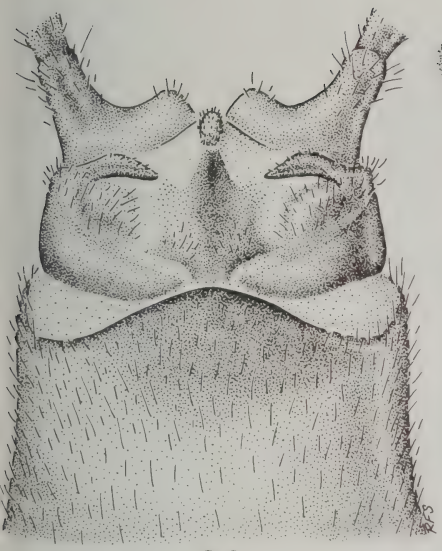


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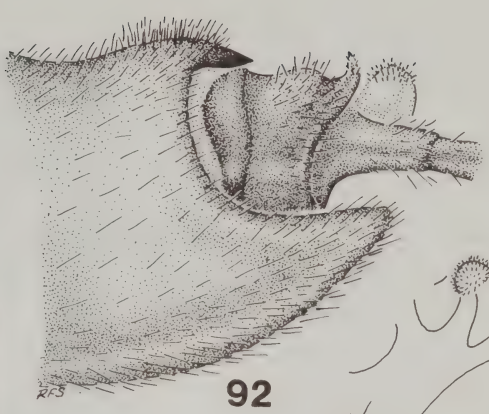


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Figs. 91–97. *Suwallia pallidula*: (91) male terminalia, dorsal; (92) male terminalia, lateral; (93) epiproct, dorsolateral; (94) aedeagus, dorsal; (95) aedeagus and terminalia, lateral; (96) female terminalia, ventral; (97) female terminalia, lateral.

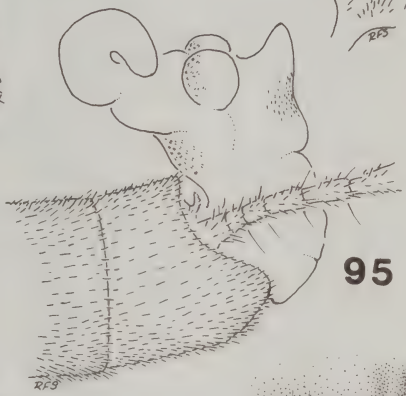


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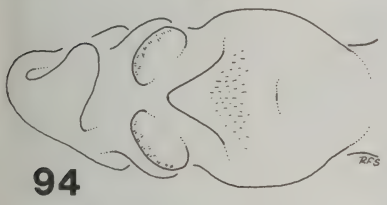


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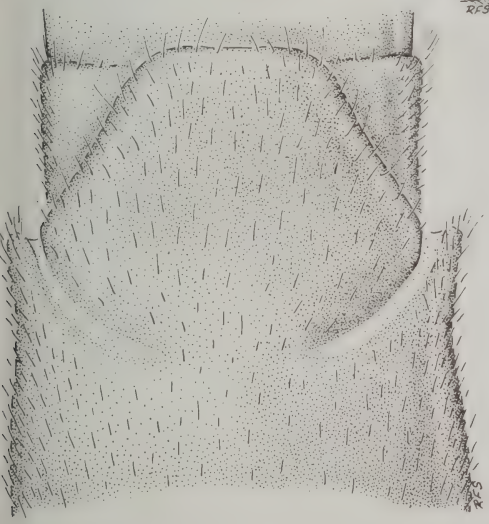
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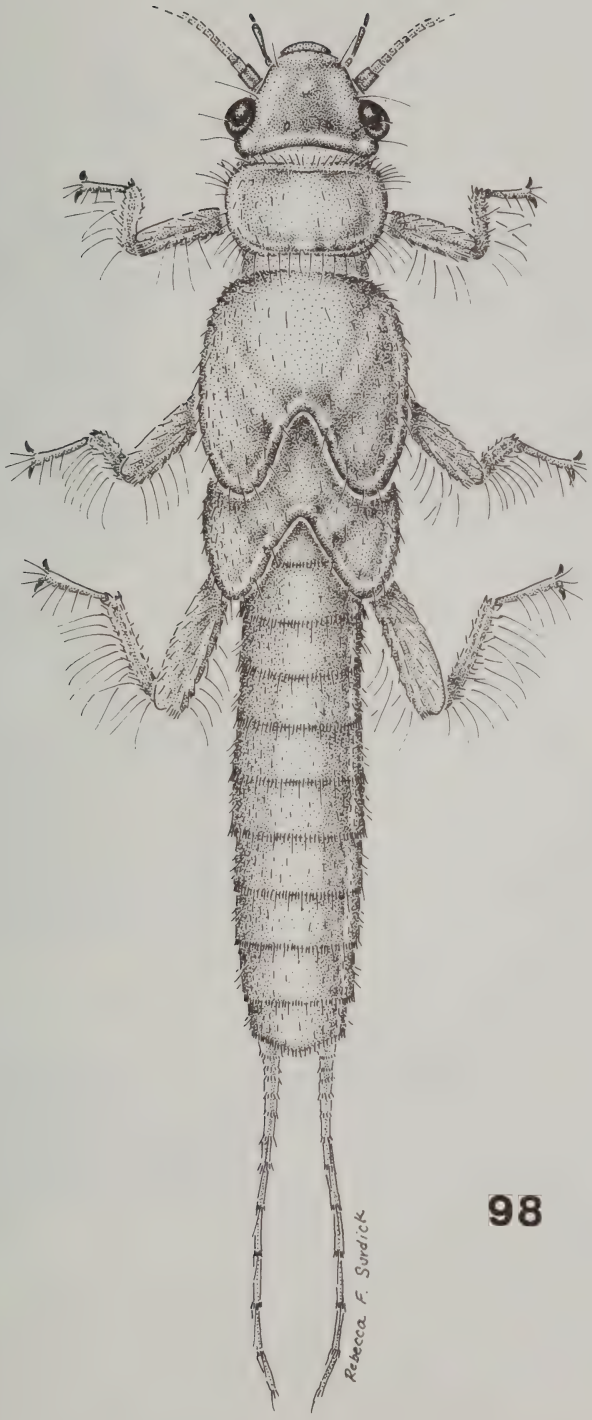


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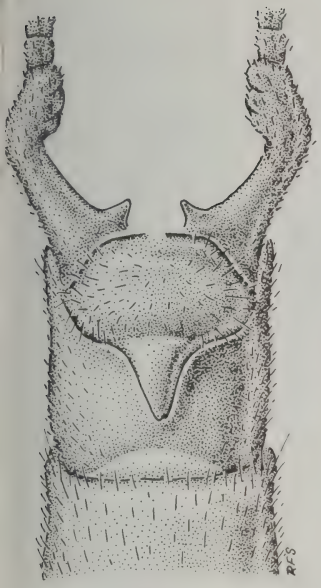


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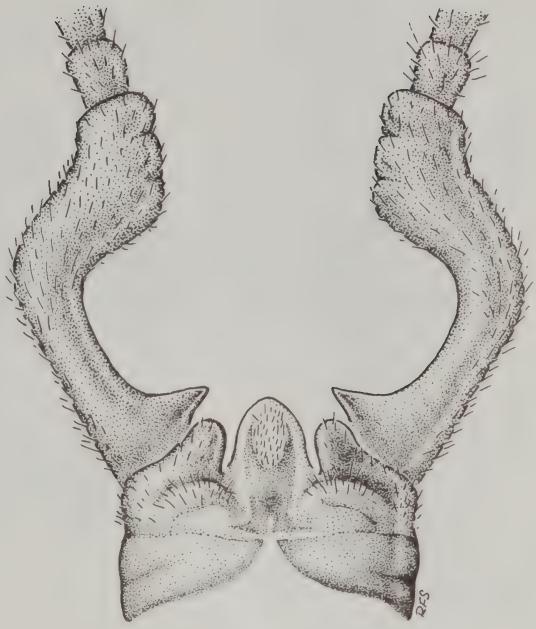
Fig. 98. *Suwallia pallidula* larva.


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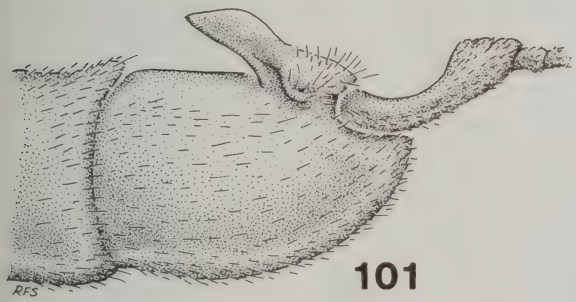
Figs. 99–103. *Neaviperla forcipata*: (99) male terminalia, dorsal; (100) male segment 10 and cerci, dorsal; (101) male terminalia, lateral; (102) male segment 10 and cercus, lateral; (103) epiproct, dorsolateral.



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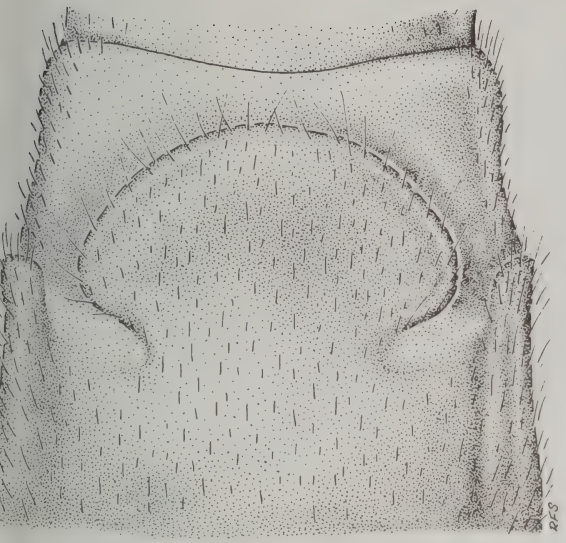


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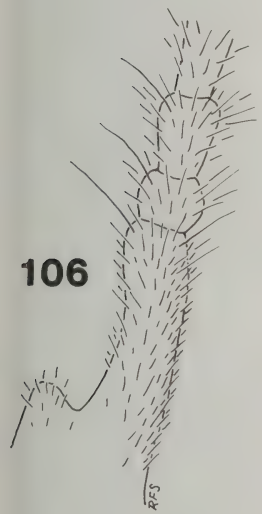
Figs. 104–108. *Neaviperla forcipata*: (104) female terminalia, ventral; (105) female terminalia, lateral; (106) female cercus; (107) aedeagus, dorsal; (108) aedeagus and terminalia, lateral.



104



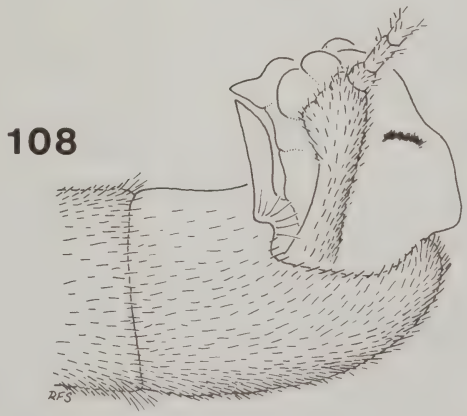
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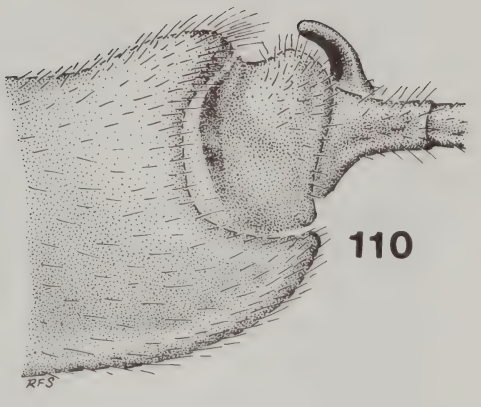


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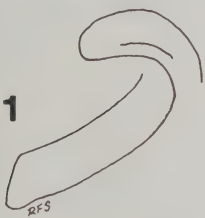
Figs. 109–115. *Triznaka pintada*: (109) male terminalia, dorsal; (110) male terminalia, lateral; (111) epiproct, dorsolateral; (112) aedeagus and terminalia, lateral (major spinulae patterns illustrated); (113) aedeagus, ventral; (114) aedeagus, dorsal; (115) posterior margin of sternum 7, male.



109



110



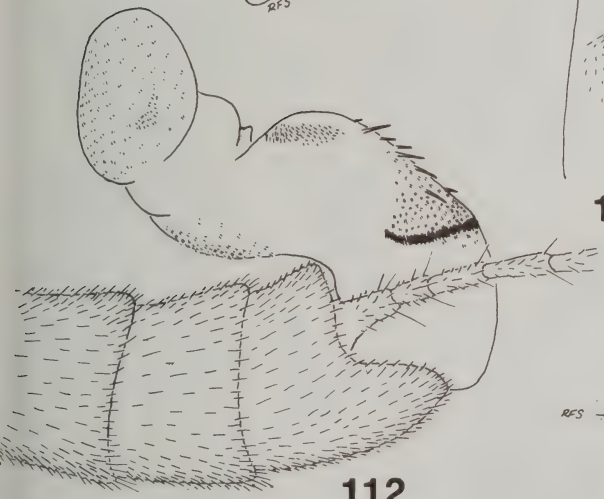
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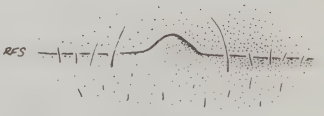
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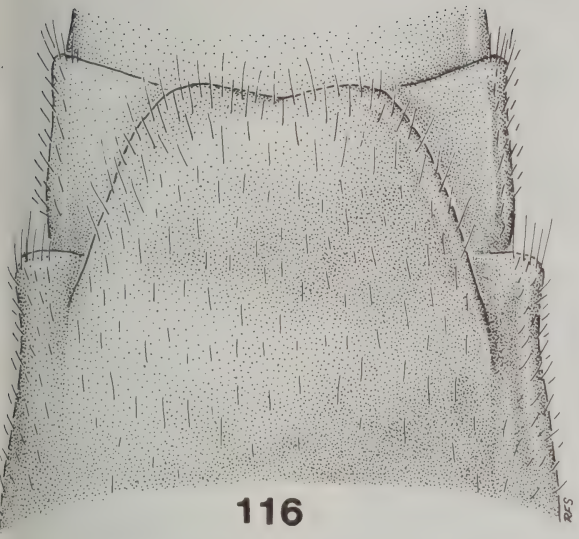


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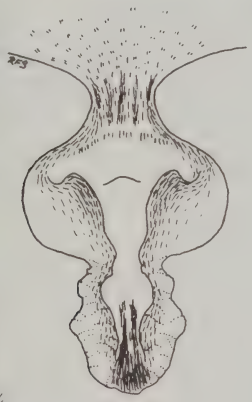
Figs. 116–121. *Triznaka pintada*: (116) female terminalia, ventral; (117) female terminalia, lateral; (118) female terminalia, illustrating location of vagina, ventral; (119) vagina, ventral (spines located on inside wall); (120) vagina, ventral, expanded; (121) vagina, lateral, with bulblike seminal receptacle and radiating accessory glands.



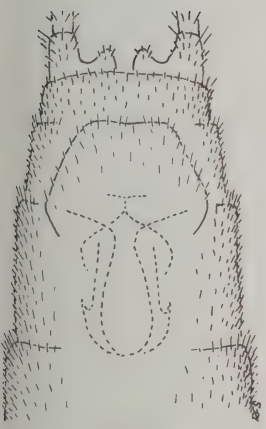
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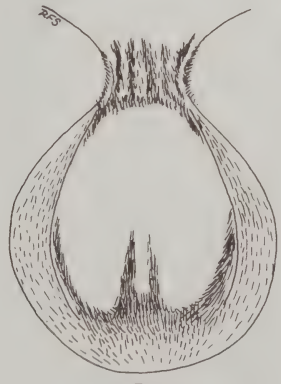
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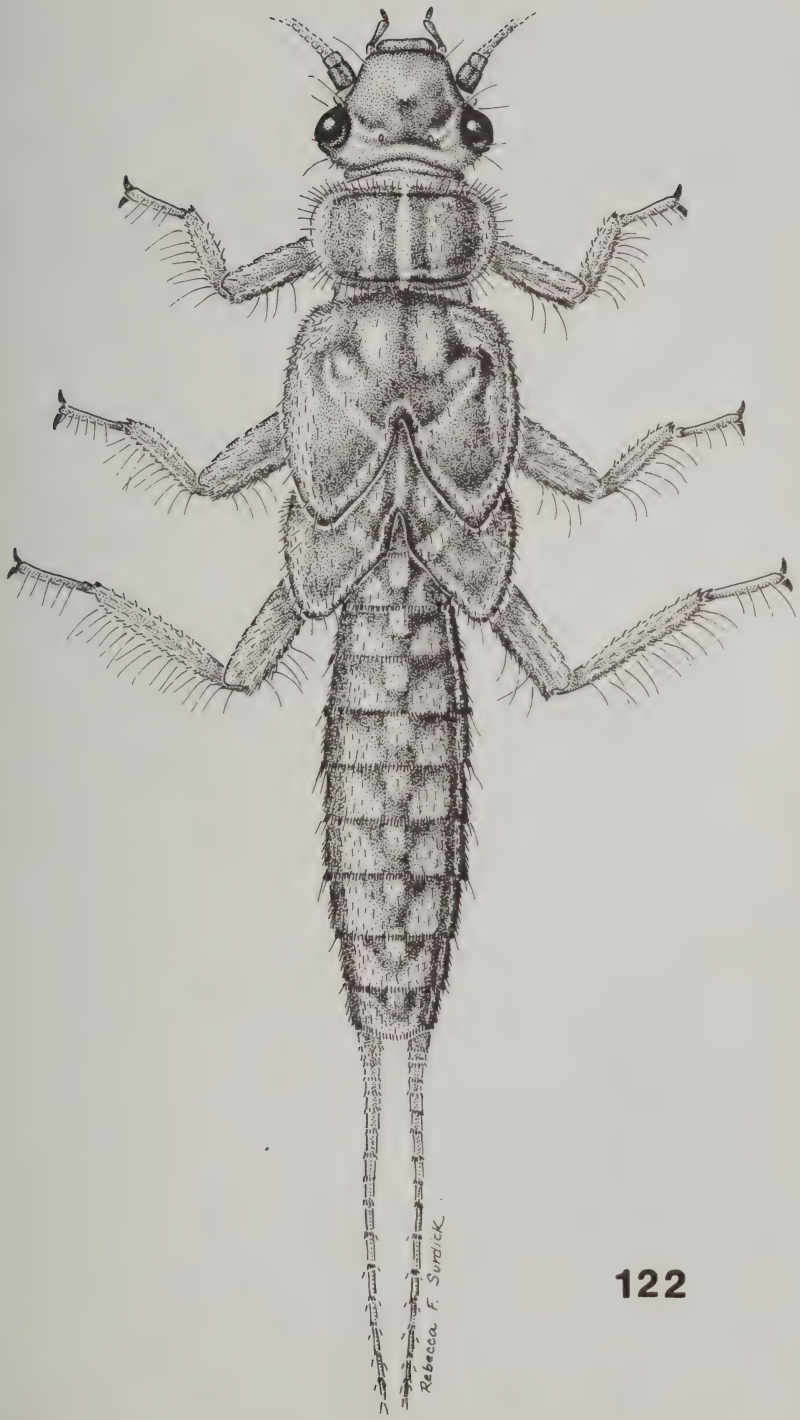


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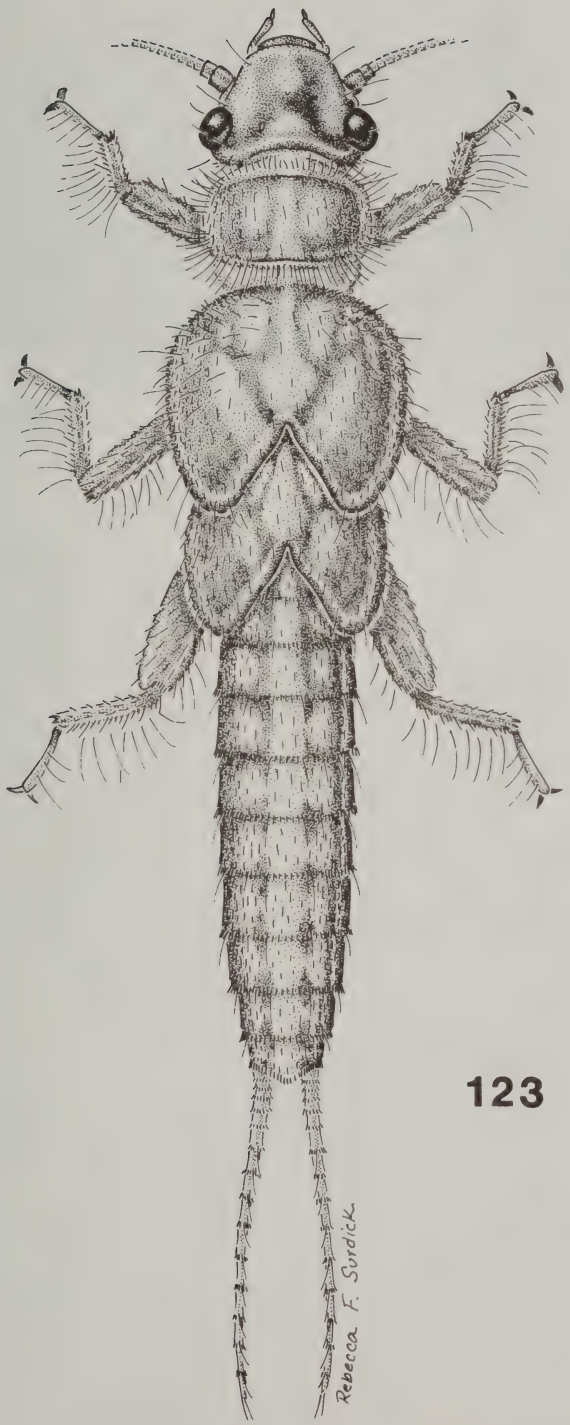
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Fig. 122. *Triznaka pintada* larva.



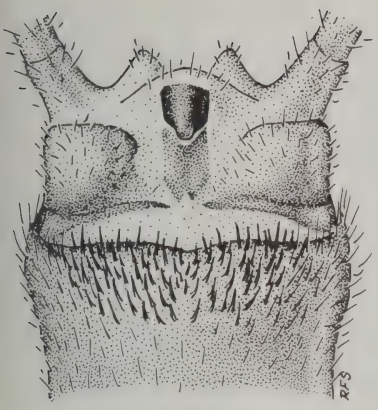
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Fig. 123. *Triznaka signata* larva.

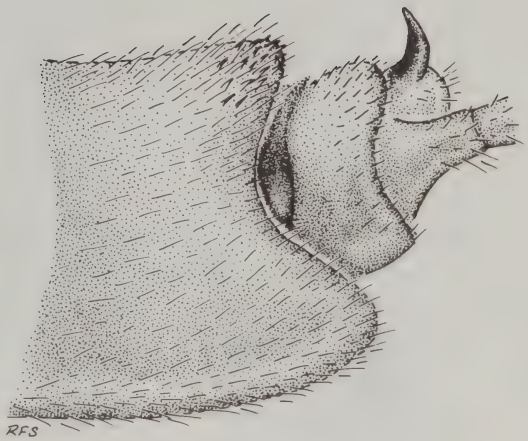


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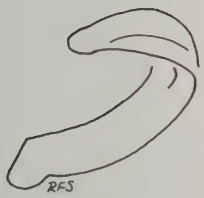
Figs. 124–129. *Plumiperla diversa*: (124) male terminalia, dorsal; (125) male terminalia, lateral; (126) epiproct, dorsolateral; (127) aedeagus and terminalia, lateral (major spinulae patterns illustrated); (128) aedeagus, ventral; (129) aedeagus, dorsal.



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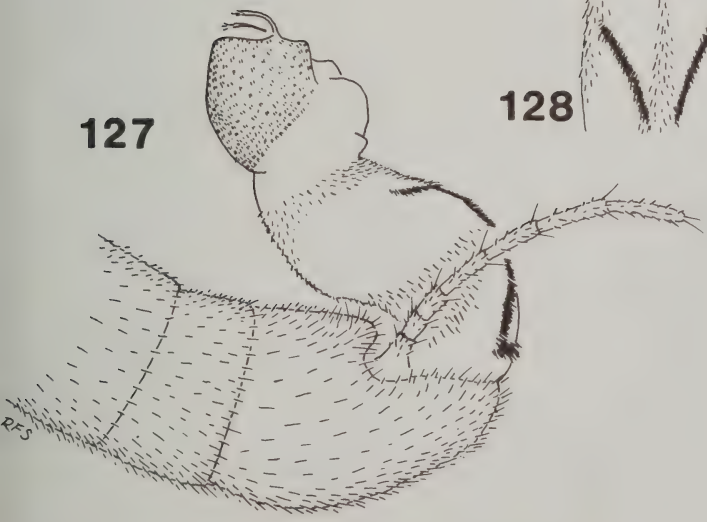


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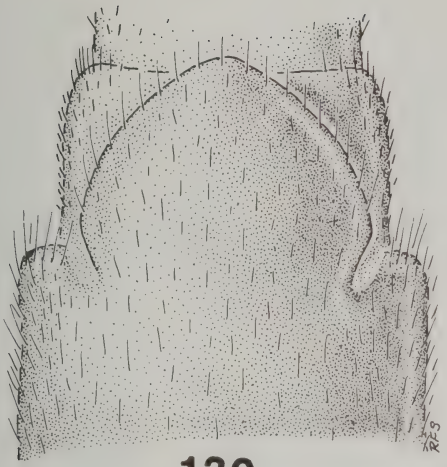


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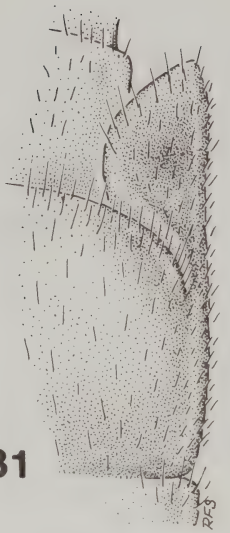
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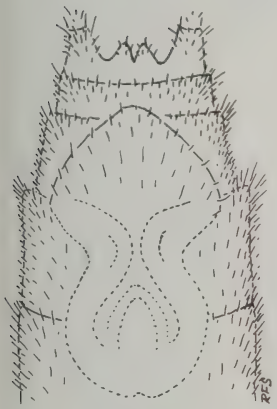
Figs. 130–135. *Plumiperla diversa*: (130) female terminalia, ventral; (131) female terminalia, lateral; (132) female terminalia, illustrating location of vagina, ventral; (133) vagina, lateral, with bulblike seminal receptacle and radiating accessory glands; (134) vagina, lateral, expanded (spines located on inside walls); (135) vagina, ventral.



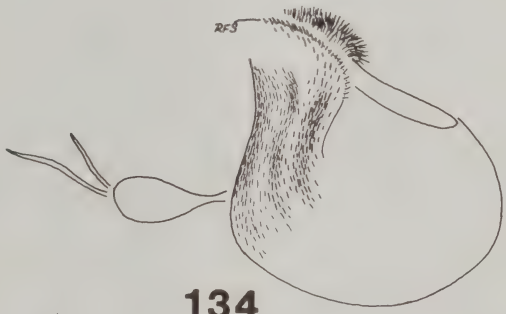
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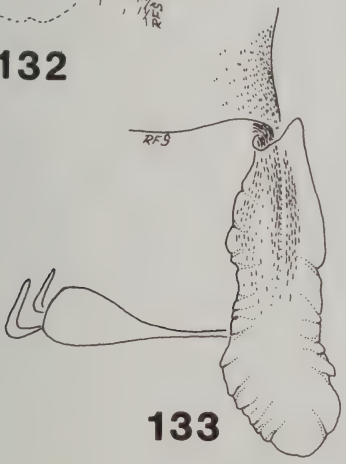
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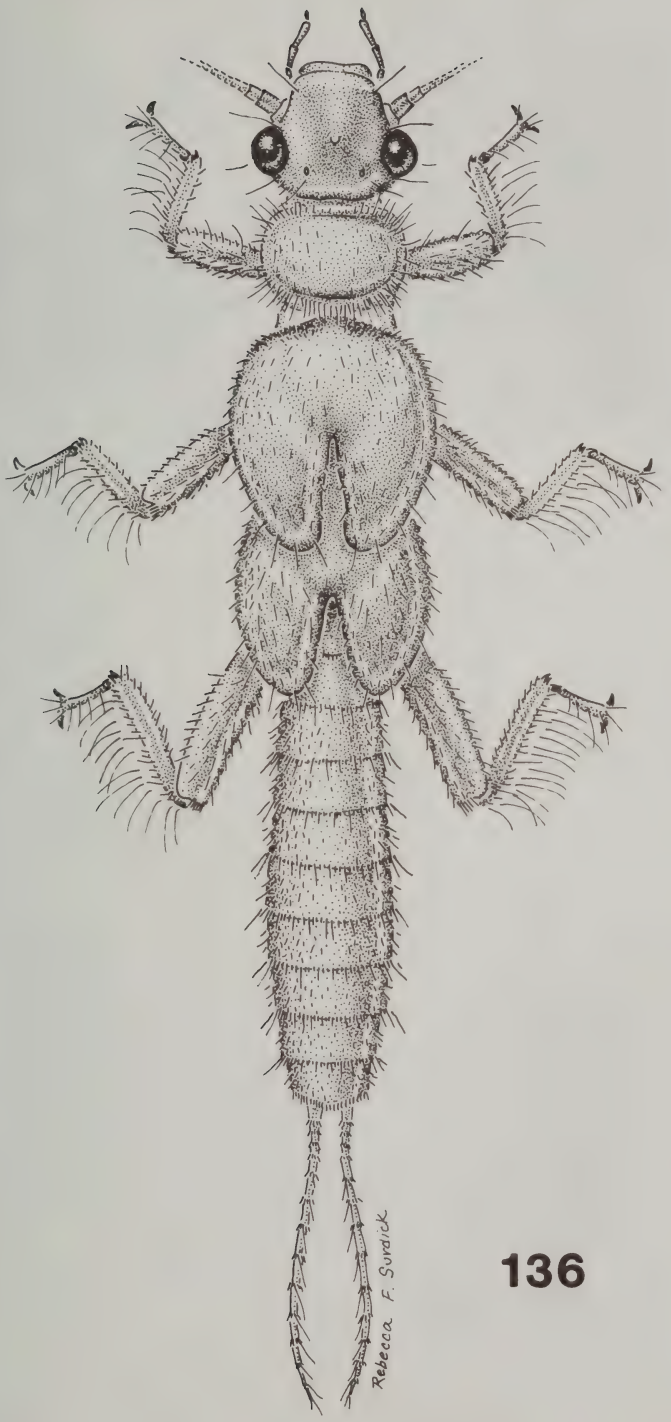


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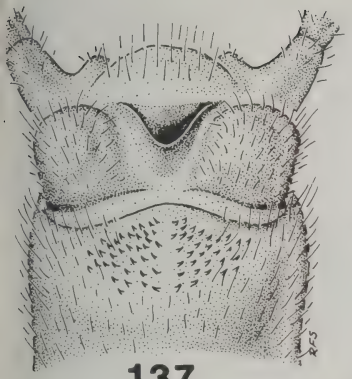
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Fig. 136. *Plumiperla diversa* larva.



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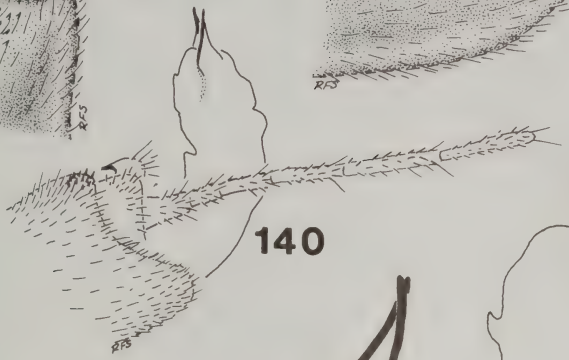
Figs. 137–145. *Haploperla brevis*: (137) male terminalia, dorsal; (138) male terminalia, lateral; (139) epiproct, dorsolateral; (140) aedeagus and terminalia, lateral; (141) aedeagus, apex; (142) skeletal rods of aedeagus; (143) aedeagus, lateral (examples of spinulae illustrated); (144) female terminalia, ventral; (145) female terminalia, lateral.



137



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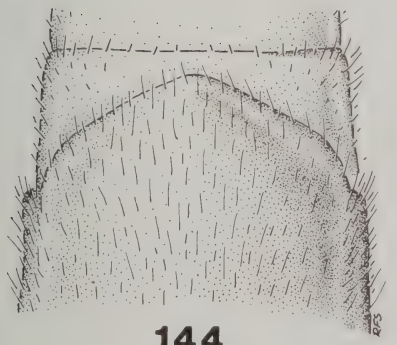
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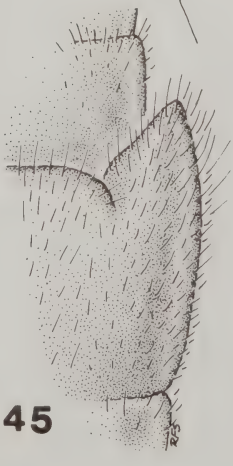
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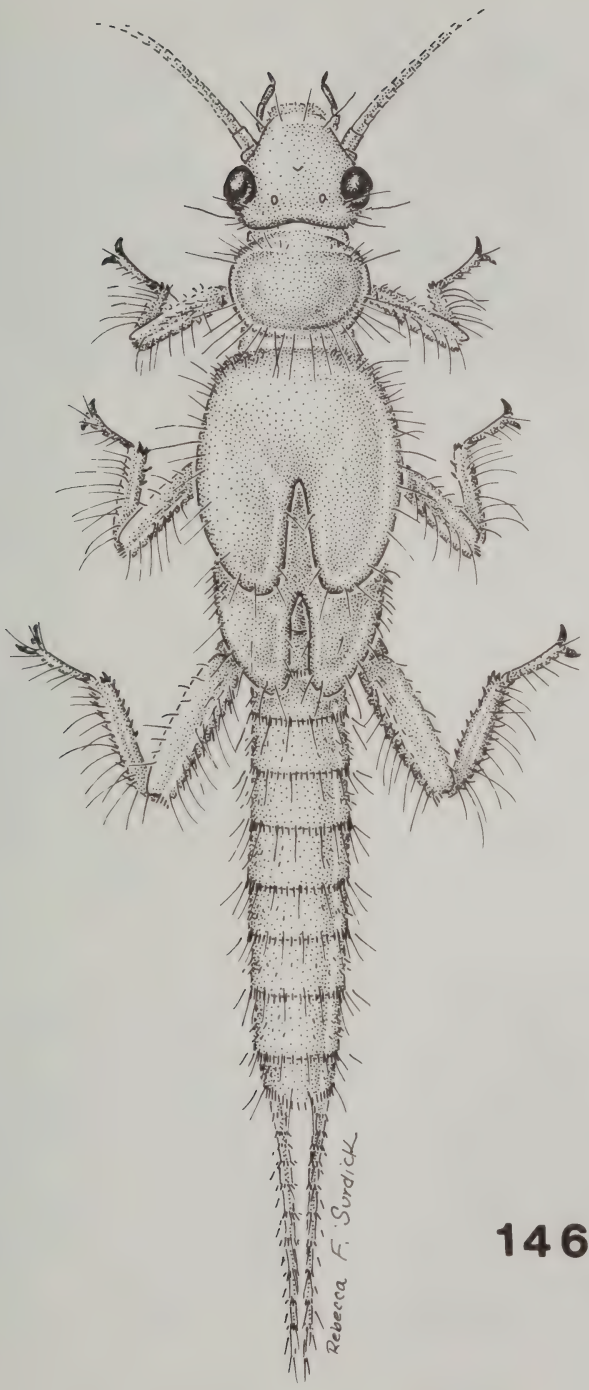


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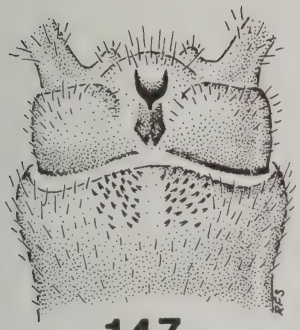


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Fig. 146. *Haploperla brevis* larva.

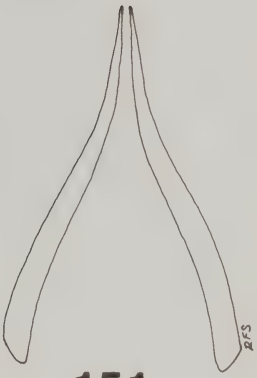

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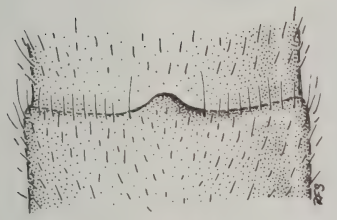
Figs. 147–153. *Rasvena terna*: (147) male terminalia, dorsal; (148) male terminalia, lateral; (149) epiproct, dorsolateral; (150) posterior margin of sternum 7, male; (151) skeletal rods of aedeagus; (152) female terminalia, ventral; (153) female terminalia, lateral.

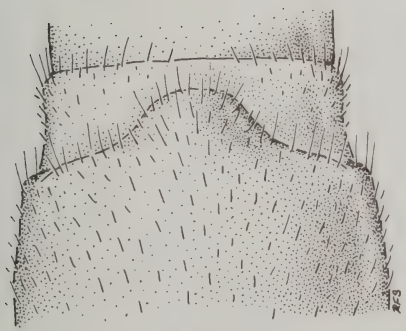

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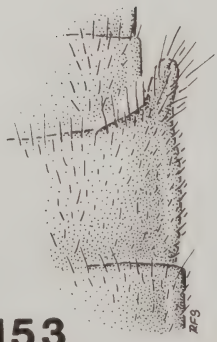
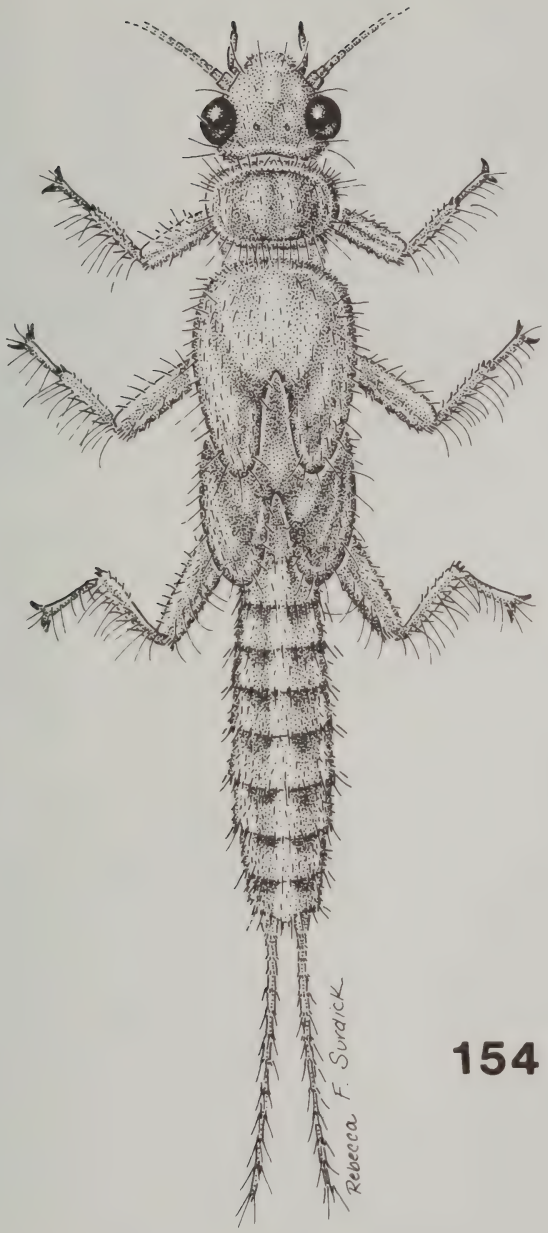
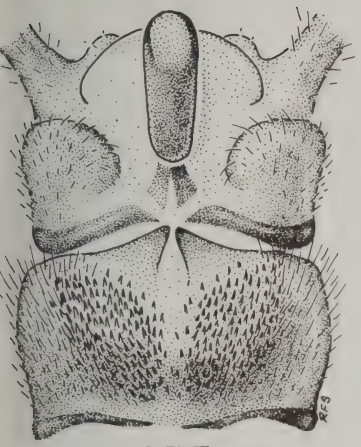

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Fig. 154. *Rasvena terna* larva.


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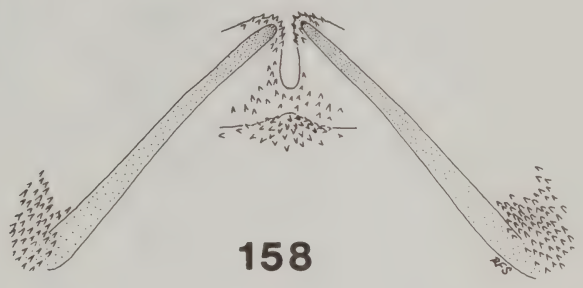
Figs. 155–160. *Chloroperla* s. l. *ovibovis*: (155) male terminalia, dorsal; (156) male terminalia, lateral; (157) epiproct, dorsolateral; (158) skeletal rods of aedeagus; (159) female terminalia, ventral; (160) female terminalia, lateral.



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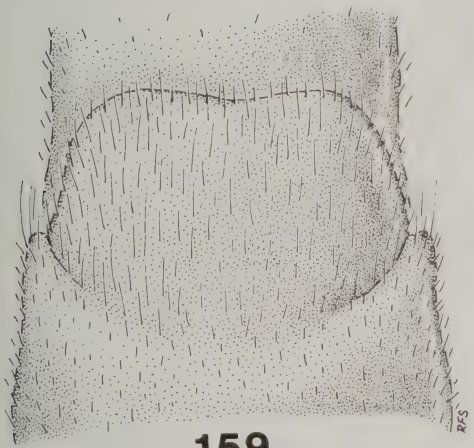
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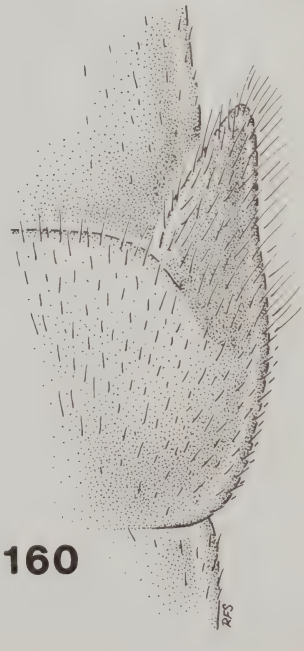
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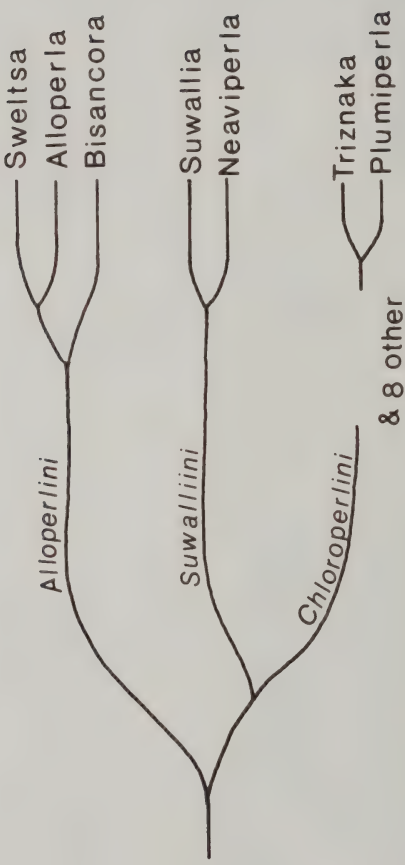


Fig. 161. Phylogenetic tree.

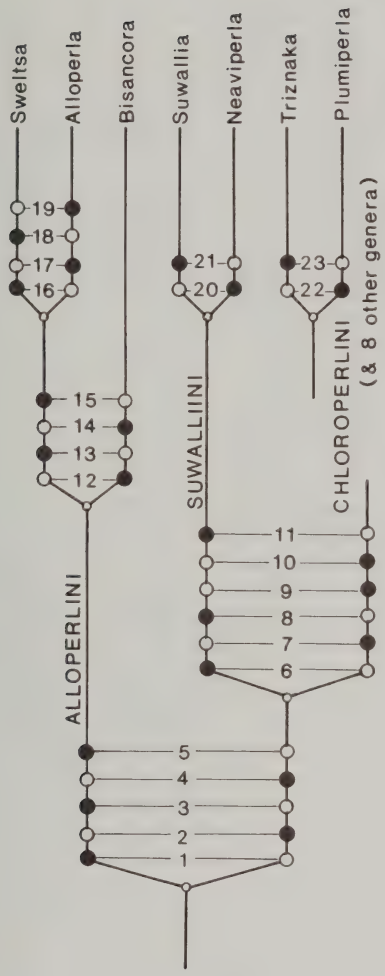


Fig. 162. Phylogenetic scheme.

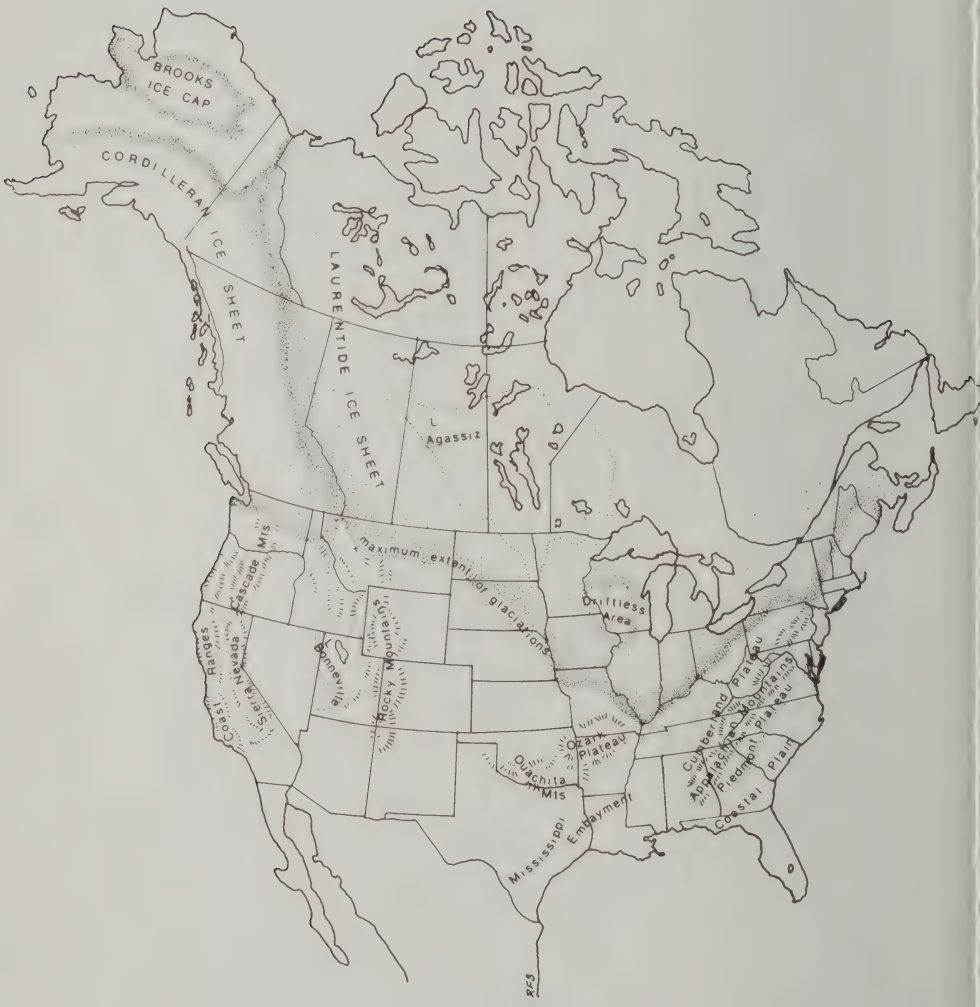


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A Note on the Author

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Introduction

According to Nowak and Paradiso (1983), there are 9 recent families, 79 genera, and 192 species in the mammalian order Artiodactyla. This order includes both the ruminants and the swine. Levine and Ivens (1970) described 102 named species of coccidia from ruminants, including 97 of *Eimeria*, 4 of *Isospora*, and 1 of *Wenyonella*. They said that *Eimeria*, the commonest genus, had been described from 30% of the 87 genera and 21% of the 188 species of ruminants, but that its location in the host was known only for 17 species of *Eimeria*, and that the endogenous stages were known for only 15 species and the presumably complete life cycles for only 2. Quite a few papers have been written on the coccidia of artiodactyls since that time, and the present monograph brings our information up to date. It includes many reports not given by Levine and Ivens (1970). In addition, it includes both ruminants and swine. Further, it includes not only the classical coccidia (family Eimeriidae) but also members of the family Sarcocystidae (*Sarcocystis, Toxoplasma,* and *Besnotita*), which were found to be coccidia after our previous monograph had been written. Because this monograph is essentially an extension of the one by Levine and Ivens (1970), no illustrations from that monograph are reproduced herein.

General accounts of the taxonomy, life cycles, and structure of coccidia have been given by Levine and Ivens (1981) and Levine (1982) and will not be repeated here. Scholtyseck (1979) reviewed their fine structure, and Long (1982) edited a review of the whole group.

This monograph is a contribution from the College of Veterinary Medicine and the Agricultural Experiment Station, University of Illinois, Urbana. It was supported in part by National Science Foundation grants GB-30800X and BMS71-01294X and National Institutes of Health grant AI-15367.

There is considerable confusion about the nomenclature of the species of *Sarcocystis* in domestic animals. The names that we believe correct have been given by Levine (1985).

The figure numbers are a continuation of those in the monograph by Levine and Ivens (1970). The appropriate figure numbers in that monograph are given following the names of the protozoan species to which they apply.

Systematic Section

The order and names of families, genera, and species of the Artiodactyla are those of Walker et al. (1975). The known species of coccidia are discussed below. If some feature of a coccidian species is unknown, the heading has been omitted for the sake of economy. Geographic distribution has been omitted because it may not be complete. Sporulation occurs outside the host's body in *Eimeria, Isospora,* and *Toxoplasma,* and in the small intestine in *Sarcocystis.* Sporulation time has been omitted because it depends upon many factors that are ordinarily not stated. No illustrations given in our 1970 monograph are included, but those in the present monograph are numbered consecutively to follow them. Reports of prevalence have also been omitted, because prevalence varies markedly from one place to another.

Host Family SUIDAE

Host Genus Sus

***Eimeria almaataensis* Musaev, 1970**

Synonyms. Eimeria debliecki Douwes, 1921 of Svanbaev (1958) in *Sus scrofa; E. almataensis* Musaev, 1970 of Svanbaev (1979).

Type Host. Wild pig *Sus scrofa.*

Oocyst Structure. Ovoid, 26–33 x 21–28 (mean 30 x 24) μm, with "double-contoured," rough, somewhat thin at one end, yellow-green to yellow-brown wall 1.5–2.1 μm thick, with polar granule, without residuum. Sporocysts ovoid, 13.5–16 x 6–8 (mean 15 x 7) μm, without residuum. Sporozoites spherical, 5.1 μm in diameter (?).

Remarks. We are not sure whether this is a valid species. Svanbaev

(1979) failed to transmit it from the wild pig to only one domestic piglet.

***Eimeria betica* Martinez and Hernandez, 1973**

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Cylindrical, sometimes ellipsoidal or spherical, salmon, 20–28 x 10–14 (mean 23 x 12.5) μm, with smooth wall 0.8–1.1 μm thick, with micropyle 5.2 μm in diameter without collar, with residuum, without polar granule. Sporocysts ovoid, 8–14 x 4–6 (mean 11 x 5) μm, with Stieda body and residuum. Sporozoites vermiform, 8–9 μm long.

Remarks. This species was named in an abstract. See Martinez, Hernandez and Calero (1974) for a more complete description.

***Eimeria debliecki* Douwes, 1921** (Fig. 295)

Synonyms. Coccidium suis Jaeger, 1921; *Eimeria brumpti* Cauchemez, 1921 in part; *E. jalina* Krediet, 1921; *E. scrofae* Galli-Valerio, 1935.

Type Host. Domestic pig *Sus scrofa.*

Other Host. Wild boar *Sus scrofa.*

Location. Epithelial cells of anterior small intestine; distal part of villi.

Oocyst Structure. Usually ellipsoidal, sometimes cylindrical, occasionally ovoid, 20–30 x 14–21 (mean 25 x 17) μm, with a smooth, colorless, 2-layered wall 1 μm thick, without micropyle or residuum, with polar granule. Sporocysts elongate ovoid, often flattened on one side, 13–20 x 5–7 (mean 17 x 6.5) μm, with a very thin wall except near the large end, with distinct Stieda body which is unusual in being excentrically located, with large residuum. Sporozoites vermiform, with one end rounded and the other pointed, lying length-wise head to tail in sporocysts, with 2 clear globules. Excysted sporozoites 14–20 x 3–4 (mean 18 x 3) μm.

Merogony. The parasites are in the distal part of the columnar epithelial cells of the tips of the villi in the small intestine. The first-generation meronts are in the 2 meters posterior to the bile duct, and the second-generation meronts in the 4 meters posterior to the bile duct. Both are anterior to the host cell nucleus. The first-generation meronts mature in 2 days or more and contain 16 merozoites and a

large polar residuum. They are 8–12 μm in diameter and their merozoites are 12–15 x 1.8 μm, vermiform, with a pointed anterior end and a rounded posterior one. Most appear at 60 hours, but some can be seen as late as 120 hours.

The second-generation meronts mature in 48 hours, at which time they are 13–16 x 10–15 μm and contain 32 merozoites and sometimes a small amount of residual material. The second-generation merozoites are 6–8 x 1.8 μm, pointed at the anterior end and rounded at the posterior end (Vetterling, 1966a).

Gamogony. According to Vetterling (1966a), the gamonts are in the 6 meters of the small intestine posterior to the bile duct; they are in the distal part of the columnar epithelial cells of the tips of the villi, anterior to the host cell nucleus. The microgamonts mature ahead of the macrogametes, in 120 hours, at which time they are 9–14 x 7–9 μm and produce many biflagellate microgametes 5–6 x 0.6 μm. The macrogametes mature more than 120 hours after inoculation. When mature, they are 12–16 x 9–13 μm and have a layer of wall-forming bodies (plastic granules) around their periphery.

Prepatent Period. 156 hours (Vetterling, 1965; Mandrussov, 1969).

Patent Period. 118 hours (Vetterling, 1965).

Pathogenicity. Boch and Wiesenhütter (1963) said that large numbers (500,000 oocysts or less) caused catarrhal exudation from the middle and posterior jejunum of pigs 2–7 weeks old, but that smaller numbers of oocysts (20,000 or more) caused no pathogenic effects, nor did large numbers of oocysts in older pigs. According to Vetterling (1966a), this species causes no clinical signs. It was only slightly pathogenic in his study, denuding the tips of the villi and causing hyperemia of the capillaries in the lamina propria and submucosa and extensive invasion by plasma cells and eosinophilic granulocytes. He saw no gross lesions, however, in 3-month-old SPF (specific pathogen-free) pigs fed 50,000 sporulated oocysts.

Remarks. Zajicek and Pav (1972) speculated that dung beetles might be involved in spreading the coccidia.

***Eimeria guevarai* Romero and Lizcano, 1971** (Fig. 298)

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Piriform, 26–32 x 15–19 (mean 28 x 16) μm, with smooth, slightly tinted, 2-layered wall, without micropyle or re-

siduum, with polar granule. Sporocysts elongate ovoid, 9–11 x 6–8 (mean 10 x 7) μm, with Stieda body and residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with a clear globule at one end.

***Eimeria ibrahimovae* Musaev, 1970**

Synonyms. Eimeria scabra Henry, 1931 of Svanbaev (1958) in *Sus scrofa; E. ibragimovae* Musaev, 1970 of Svanbaev (1979).

Type Host. Wild pig *Sus scrofa.*

Oocyst Structure. Ovoid or broadly ovoid, 24–31 x 20–26 (mean 25 x 22) μm, with smooth, yellow-green to yellow-brown, "double-contoured" wall 1.2–1.7 μm thick, with polar granule. Sporocysts ovoid, 7–15 x 5–7 (mean 10 x 6) μm, with small residuum (?). Sporozoites 5 μm long.

Remarks. We are not sure whether this is a valid species. Svanbaev (1979) failed to transmit it from the wild pig to a domestic piglet.

***Eimeria neodebliecki* Vetterling, 1965** (Fig. 293)

Synonyms. Eimeria brumpti Cauchemez, 1921 in part; *E. debliecki* Douwes, 1921 in part.

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Ellipsoidal, occasionally ovoid, 17–26 x 13–20 (mean 21 x 16) μm, with smooth, colorless, 2-layered wall 0.7–1.4 μm thick, without micropyle or residuum, with polar granule. Sporocysts ovoid, 9–14 x 5–8 μm, with residuum and prominent Stieda body. Sporozoites vermiform, with one end rounded and the other pointed, lying lengthwise head to tail in sporocysts, with 2 clear globules (Vetterling, 1965; Shrivastav and Shah, 1968).

Prepatent Period. 240 hours (Vetterling, 1965).

Patent Period. 144 hours (Vetterling, 1965).

***Eimeria perminuta* Henry, 1931** (Fig. 292)

Synonyms. Eimeria perminuta var. *mathurai* Mishra, 1967.

Type Host. Domestic pig *Sus scrofa.*

Other Host. Wild boar *Sus scrofa.*

Oocyst Structure. Spherical to subspherical, 12–20 x 9–17 μm, with rough, yellow, 2-layered wall 1 μm thick, without micropyle or residuum, with polar granule. Sporocysts ellipsoidal to ovoid, 6–12 x 4–6 μm, with finely granular residuum and prominent Stieda body. Spo-

rozoites vermiform, lying lengthwise head to tail in sporocysts, each with 2 clear globules (Vetterling, 1965; Mishra, 1967; Shrivastav and Shah, 1968).

***Eimeria polita* Pellérdy, 1949** (Fig. 296)

Synonyms. Eimeria cerdonis Vetterling, 1965; *E. debliecki* Douwes, 1921 in part.

Type Host. Domestic pig *Sus scrofa.*

Other Host. Wild boar *Sus scrofa.*

Location. Epithelium of villi distal to the host cell nucleus in the jejunum and ileum (Centurier, 1970).

Oocyst Structure. Ellipsoidal, rarely ovoid, 17–36 x 13–24 μm, colorless, yellowish brown or pinkish brown, smooth, slightly rough or pitted, with a 2-layered wall 1.0–1.5 μm thick, with imperceptible or rarely seen micropyle, without residuum, with polar granule in about 50%. Sporocysts ellipsoidal to ovoid, 15–19 x 6–9 μm, with a residuum and Stieda body. Sporozoites vermiform, with one end rounded and the other pointed, lying lengthwise head to tail in sporocysts, usually with 1–2 clear globules (Pellérdy, 1949; Lesser and Davis, 1958; Vetterling, 1965; Waddell, Hoyte and Daniel, 1971; Shrivastav and Shah, 1968).

Rommel (1970) found that the size of the oocysts of a pure strain of *E. polita* depended on the conditions of infection. They became larger during the course of the patent period and were relatively large when the infective dose was small, in the absence of immunity, and in older hosts. The oocysts seen by Centurier (1970) (and derived from a single oocyst) were 13–19 x 11–12 (mean 16 x 12) μm.

Merogony. Centurier (1970) said that merogony occurs in the partially invaginated epithelial lining of the tips of the villi of the entire jejunum and ileum, the posterior 9/10 of the small intestine being the most heavily infected. She assumed that there were 2 meront generations, even though she could not indisputably differentiate the meronts that appeared on days 5 and 7.

On day 4 mature meronts are 14–24 x 11–23 (mean 17 x 14) μm, and contain 16–30 (mean 22) sickle-shaped merozoites 9–22 x 1.5–3 (mean 14 x 2) μm in fresh preparations. On days 5 and 6 mature meronts are 14–23 x 12–20 (mean 19 x 16) μm and contain 15–30 (mean 20) merozoites 10–15 x 1.5–3 (mean 13.5 x 2) μm. In unstained smears, the meronts are 12–25 x 18–23 (mean 18 x 15) μm.

On day 7, about 10% of the mature meronts have a more or less central residuum 8–9 μm in diameter. She saw some meronts that appeared different from the others. In fresh smears, they were 12–30 x 11–20 (mean 17 x 14) μm and contained granular merozoites 6–14 x 1.5–5 (mean 10 x 2) μm, being 1–2 μm shorter and thicker than the ungranulated merozoites.

Gamogony. Centurier (1970) said that the gamonts are in the same part of the intestine as the meronts. They mature on day 8 or 9. The macrogametes average 17 x 13 μm in sections and are 16–29 x 15–25 (mean 23 x 20) μm in smears; they have plastic granules around their periphery. The microgamonts are 16–29 x 13–29 (mean 22 x 19) μm, with a residuum, and produce 60–150 microgametes 2.2 x 0.6 μm (in smears). In sections, they are 12–16 x 10–13 (mean 14.5 x 12) μm. The free microgametes are 4.8 x 0.6 μm and have 2 flagella 11.4 and 6.8 μm long.

Prepatent Period. Seven to 8 days (Pellérdy, 1949; Vetterling, 1965; Rommel, 1970).

Patent Period. 144 hours (Vetterling, 1965); 8 days (Rommel, 1970).

Pathogenicity. This species is only slightly pathogenic. Rommel (1970) said that it caused temporary constipation or diarrhea when the infecting dose was not less than 200 oocysts. Centurier (1970) said that pigs given several million oocysts remained healthy. There was a slight catarrhal exudate in the last third of the small intestine and leukocytic infiltration of the propria mucosae.

Immunity. Rommel (1970a) found that inoculation of young pigs produced complete immunity against the same species for 1 month and rather strong partial immunity for at least 5 months. It also produced partial immunity against *E. scabra.*

De Andrade and Weiland (1971) found cross-reactions between *E. polita, E. scabra, E. nieschulzi, Isospora felis* and *Toxoplasma gondii* with the microagar precipitation test. They found only specific reactions with the indirect fluorescent antibody and Sabin-Feldman tests using *Sarcocystis tenella* and *T. gondii* antigens.

Remarks. Rommel (1970) found that the following numbers of oocysts were produced per oocyst fed to 10–35 kg pigs: 200 oocysts fed, 213,000 oocysts produced per oocyst fed; 20,000 oocysts fed, 16,800 oocysts produced per oocyst fed; 1.5 million oocysts fed, 224 oocysts produced per oocyst fed; 3.5 million oocysts fed, 34 oocysts produced per oocyst fed.

***Eimeria porci* Vetterling, 1965** (Fig. 299)

Synonym. Eimeria debliecki Douwes, 1921 in part.

Type Host. Domestic pig *Sus scrofa.*

Location. Lower jejunum and ileum.

Oocyst Structure. Ovoid to piriform, 18–27 x 13–18 μm, with a smooth, colorless, 2-layered wall 0.9–1.2 μm thick, with or without micropyle 2–3 μm wide, without residuum, with polar granule. Sporocysts ovoid, 8–12 x 6–8 μm, with sparse residuum and indistinct Stieda body. Sporozoites corpulent, lying at ends of sporocysts or lengthwise head to tail in them, with 1–2 clear globules (Vetterling, 1965; Shrivastav and Shah, 1968).

Merogony. Wheat and Fitzgerald (1978) studied the endogenous life cycle of this species, using 4- to 5-week-old pigs infected with 200,000 sporulated oocysts each. The asexual cycle occurs between the host cell nucleus and basement membrane of the epithelial cells of the lower jejunum and ileum. There are 2 asexual generations, the first one 1–3 days after inoculation and the second, 3–6 days after inoculation.

Gamogony. Wheat and Fitzgerald (1978) found the sexual stages below the host cell nucleus in the epithelial cells of the villi of the lower jejunum and ileum. They saw young gamonts 5 days after inoculation.

Prepatent Period. 5–6 days (Vetterling, 1965; Wheat and Fitzgerald, 1978).

Patent Period. 6 days (Vetterling, 1965).

***Eimeria residualis* Martinez and Hernandez, 1973**

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Ellipsoidal, exceptionally cylindroid or ovoid, 28–36 x 14–24 (mean 32 x 20) μm, with smooth, ochraceous wall 1.3–1.5 μm thick, with collared micropyle 5 μm in diameter, with large residuum; apparently without polar granule. Sporocysts ellipsoidal, 11–17 x 6–8 (mean 14 x 7.5) μm, with Stieda body and residuum. Sporozoites 13 μm long.

Remarks. This species was named in an abstract. See Martinez, Hernandez and Calero (1974) for a more complete description.

***Eimeria scabra* Henry, 1931** (Fig. 308)

Synonyms. Eimeria debliecki Douwes, 1921 in part; *E. romaniae* Donciu, 1961; *E. scarba* Yakimoff and Matikaschwili, 1932 *(lapsus calami).*

Type Host. Domestic pig *Sus scrofa.*

Other Host. Wild boar *Sus scrofa.*

Location. Epithelial cells of villi and necks of crypts of posterior small intestine. Pastuszko (1966) said it was also in the cecum and colon.

Oocyst Structure. Ovoid to ellipsoidal, rarely asymmetrical, 23–45 x 17–28 μm, with a rough, striated, yellow to brown, 2-layered wall 1.5–3.0 μm thick, with micropyle and polar granule, without residuum. Sporocysts ovoid, 12–20 x 6–11 μm, with residuum and prominent Stieda body. Sporozoites vermiform, with one end rounded and the other pointed, lying lengthwise head to tail in sporocysts, with 2 clear globules (Vetterling, 1965; Boch, Pezenburg and Rosenfield, 1961; Shrivastav and Shah, 1968; Rommel, 1970; Waddell, Hoyt and Daniel, 1971).

Merogony. Rommel and Ipczynski (1967) studied the life cycle of this species, using a pure strain. All stages were in the epithelial cells of the distal third of the villi in the posterior half of the small intestine. There were 3 meront generations. The first-generation meronts matured 3 days after inoculation; they were 16 x 13 μm and contained 16–24 merozoites and usually no residuum. The second-generation meronts matured 5 days after inoculation; they were 16 x 12 μm and contained 14–22 merozoites; about 40% of them had a residuum. The third-generation meronts matured 7 days after inoculation; they were 21 x 16 μm and contained 14–28 merozoites; about 90% of them had a residuum. The merozoites of all 3 generations were arranged like the sections of an orange.

Gamogony. The macrogametes are 18 x 12 μm and the microgamonts are 17 x 13 μm in sections. The latter contain many biflagellate microgametes 2.5–4.4 μm long (Rommel and Ipczynski, 1967).

Prepatent Period. 7–10 days (Vetterling, 1965; Pastuszko, 1966; Rommel and Ipczynski, 1967; Rommel, 1970; Mandrussov, 1969).

Patent Period. 4–8 days (Vetterling, 1965; Rommel and Ipczynski, 1967; Rommel, 1970).

Pathogenicity. Rommel (1970) said that this species caused temporary constipation or diarrhea when the infecting dose was not less than 200 oocysts. Pastuszko (1966) said that it caused hyperemia of the mucosa and even diffuse necrotic foci in the colon and cecum.

Immunity. Rommel (1970a) found that inoculation of young pigs with *E. scabra* produced complete immunity against the same species

that lasted 4 months, and strong partial immunity lasting at least 5 months. It also produced partial immunity against *E. polita*. Rommel and Heydorn (1971) were unable to immunize pigs with mesenteric lymph node lymphocytes from immune pigs.

Remarks. Rommel (1970) found that the following numbers of oocysts were produced per oocyst fed in 10–35 kg pigs: 1 oocyst produced 7.6 million oocysts; 200 oocysts produced 3.14 million oocysts per oocyst fed; 20,000 oocysts produced 34,400 oocysts per oocyst fed; 1.5 million oocysts produced 136 oocysts per oocyst fed.

***Eimeria spinosa* Henry, 1931** (Fig. 301)

Type Host. Domestic pig *Sus scrofa*.

Location. Throughout small intestine except duodenum.

Oocyst Structure. Ovoid to ellipsoidal, 14–26 x 12–21 μm, with a rough, spined, brown, 2-layered wall about 1 μm thick, without micropyle or residuum, with polar granule. Sporocysts elongate ovoid, 10–14 x 5–7 (mean 11 x 6) μm, with residuum and prominent Stieda body. Sporozoites vermiform, lying lengthwise in sporocysts, with clear globule at the large end (Vetterling, 1965; Alicata, 1946; Boch, Pezenburg and Rosenfeld, 1961).

Merogony. Wiesenhütter (1962) found numerous developmental stages from the jejunum through the ileum. They were in the villar epithelial cells, but only a few were in the crypts; sometimes they were also in the lamina propria. Mature meronts were 8–10 μm in diameter and contained more than 20 merozoites 4–6 x 1–1.5 μm with a nucleus near one end.

Gamogony. Wiesenhütter (1962) said that the gamonts were in the same location as the meronts.

Prepatent Period. 7 days (Wiesenhütter, 1962).

Pathogenicity. Wiesenhütter (1962) said that an 8-week-old pig died 11 days after having been fed 12,000 sporulated oocysts, i.e., 4 days after the beginning of the patent period. It had inflammation of the small and large intestines and fibrinous serositis of the cecum and colon.

***Eimeria suis* Nöller, 1921 (Fig. 300)**

Synonyms. Eimeria jalina (Perroncito, 1901) Neveu-Lemaire, 1912 *nomen nudum*, Krediet, 1921; *E. brumpti* Cauchemez, 1921 in part; *E. debliecki* Douwes, 1921 of *auctores* in part; *E. perminuta* Henry, 1931 of

Boch, Pezenburg and Rosenfeld (1961); *E. tuis* Nöller, 1929 of Pellérdy (1963) *lapsus calami.*

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Ellipsoidal to subspherical, 13–22 x 11–16 μm, with a colorless, smooth, 2-layered wall 0.5 μm thick, without micropyle or residuum, with a polar granule. Sporocysts elongate ovoid, 8–12 x 4–6 (mean 10 x 5) μm, with residuum and prominent Stieda body. Sporozoites vermiform, with one end rounded and the other pointed, lying lengthwise head to tail in sporocysts, with a clear globule at the rounded end (Vetterling, 1965; Waddell, Hoyt and Daniel, 1961).

Prepatent Period. 10 days (Vetterling, 1965).

Patent Period. 6 days (Vetterling, 1965).

***Eimeria* sp. Desser, 1978**

Type Host. Domestic pig *Sus scrofa.*

Location. Liver (bile duct epithelium).

Oocyst Structure. Smooth, 28–32 x 13–17 (mean 30 x 15.5) μm, without micropyle or micropylar cap. (Size apparently in fixed sections.)

Remarks. Desser (1978) found giant meronts, gamonts and oocysts in sections of the liver (bile duct epithelium) of a pig in New Zealand. He said that they belonged to the "*Eimeria debliecki* group."

***Isospora almataensis* Paichuk, 1953**

Type Host. Domestic pig *Sus scrofa.*

Location. Unknown; oocysts found in feces.

Oocyst Structure. Ovoid or spherical, mostly gray; spherical oocysts 26–34 (mean 28) μm in diameter and ovoid ones 25–32 x 23–29 (mean 28 x 26) μm, with smooth, dark brown, 3-layered wall up to 3 μm thick, without residuum. Sporocysts 12–19 x 9–12 (mean 15 x 11) μm, with residuum. Sporozoites short ovoid, 6 x 4 μm.

Remarks. Pellérdy (1965) doubted the validity of this species. He said that the oocysts looked like those of *I. lacazei* of the sparrow, whereas some resembled those of *I. suis.*

***Isospora neyrai* Romero and Lizcano, 1971** (Fig. 305)

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Ovoid or ellipsoidal, 9–17 x 6–13 (mean 13 x 9)

μm, with a 2-layered wall, without micropyle; residuum said to be present but the photomicrographs show that it may be a polar granule; polar granule not said to be present. Sporocysts ovoid or subspherical, 4–8 x 2–6 (mean 5 x 4) μm, without Stieda body, presumably with residuum. Sporozoites elongate ovoid, with clear globule.

***Isospora suis* Biester in Becker, 1934** (Fig. 294)

Synonyms. Isospora sp. Yakimoff et al., 1936.

Type Host. Domestic pig *Sus scrofa.*

Other Host. Wild boar *Sus scrofa.*

Location. Small intestine; occasionally large intestine.

Oocyst Structure. Spherical to subspherical, 17–25 x 16–21 μm, with smooth, colorless, 1-layered wall 0.5–0.7 μm thick (after sporulation, most oocysts retained their spherical shape, whereas in a few the oocyst wall was depressed between the sporocysts), without micropyle, residuum or polar granule. Sporocysts ellipsoidal, 11–14 x 8–11 (mean 13 x 9) μm, often lying against each other with one side somewhat flattened, with wall 0.2–0.4 μm thick, without Stieda body, with residuum. Sporozoites sausage-shaped, with one end somewhat more pointed than the other, 9–11 x 3–4 (mean 10 x 3) μm, with a clear subcentral nucleus often visible.

Merogony. Lindsay et al. (1981) and Matuschka and Heydorn (1982) studied merogony. Asexual stages occur in the villar epithelial cells of the small intestine and sometimes of the colon. Most are in the mid-jejunum, usually in the distal third of the villus and usually below the host cell nucleus. There are apparently 2 meront generations, but Lindsay et al. (1981) were unable to be positive about the number and wrote instead of Type I and Type II meronts and merozoites. The former were present 3 days after inoculation. They were 10–18 x 5–10 (mean 14 x 8) μm in smears and 8–13 x 4–6 (mean 10.5 x 5) μm in tissue sections and contained 2–14 merozoites 11–18 x 4–9 (mean 15 x 6.5) μm in smears, and 8–13 x 2.5–5 (mean 10 x 4) μm in sections (4–16 merozoites about 19 x 5 μm at 2 days according to Matuschka and Heydorn, 1982).

Second-generation meronts are present 4 days after inoculation. They are elongate and occur singly or in groups of 2–4 per cell. They are 12–20 x 7–12 (mean 15 x 7.5) μm in mucosal smears and 9–15 x 4–8 (mean 11 x 5) μm in tissue sections. They produce 2–16 crescent-shaped merozoites 7–12 x 2.5–5 (mean 10 x 3) μm in mucosal smears

and 4–9 x 1.5–3 (mean 6 x 2) μm in tissue sections (4–16 merozoites about 9.5 x 2.5 μm at 4 days according to Matuschka and Heydorn, 1982).

Gamogony. Lindsay et al. (1981) saw immature macrogametes and microgamonts 4 days after inoculation, and both immature and mature ones and oocysts at 5 days. The oocysts are 11–20 x 9–16 (mean 15 x 12) μm in tissue sections and 16–21 x 14–20 (mean 18 x 16) μm in mucosal smears. Matuschka and Heydorn (1982) said that after sporulation the oocysts were ellipsoidal, 19–24 x 18–21 (mean 21.5 x 19) μm, with a 1-layered, thin wall, without micropyle, residuum or polar granule. The sporocysts are ellipsoidal, 14–16 x 10–13 (mean 15.5 x 11) μm, without a Stieda body, with a residuum. The oocysts remain infective for more than 2 years. The microgametes have 2 flagella.

Prepatent Period. 5–5.5 days (Vetterling, 1965; Lindsay et al., 1981; Matuschka and Heydorn, 1982).

Patent Period. 3–8 days (Vetterling, 1965; Lindsay et al., 1981); 10–13 days (Matuschka and Heydorn, 1982).

Pathogenicity. This species causes diarrhea for some days in baby pigs and has recently been found by a number of workers to be a significant pathogen in young pigs. Stuart et al. (1980) found that 400,000 sporulated oocysts given by mouth to baby pigs caused diarrhea, dehydration, weight loss and death; diarrhea and lesions occurred in pigs given as few as 150,000 oocysts. Clinical signs and lesions developed 3–4 days after inoculation. There was mild to severe villar atrophy and necrosis of the villar epithelium, often with a diphtheritic membrane. Robinson and Morin (1982) described outbreaks of baby pig diarrhea in 66 farrowing operations in Quebec, Canada. Morbidity was variable, and mortality less than 20%. Matuschka and Männer (1981) found that infection of early-weaned pigs at 22 days of age reduced weight gains during the next 4 weeks by 20%.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species from the wild pig to 13 piglets.

Isospora sp. Shrivastav and Shah, 1968

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Subspherical to spherical, 25–26 x 25 (mean 25.5 x 25) μm, with 2-layered wall 1.2 μm thick, outer layer smooth, yel-

lowish to pale brown, inner layer dark brownish yellow, without micropyle, polar granule or residuum. Sporocysts lemon-shaped, 14 x 9 μm, with Stieda body, substiedal body and residuum. Sporozoites more or less sausage-shaped, with large clear globule at broad end.

Remarks. Shrivastav and Shah (1968) remarked that this oocyst closely resembled that of *I. lacazei* of the English sparrow and that it was probably a pseudoparasite of sparrow origin.

***Sarcocystis miescheriana* (Kühn, 1865) Labbé, 1899**

Synonyms. Synchrytium miescherianum Kühn, 1865; *Sarcocystis miescheri* Lankester, 1882; *S. suicanis* Erber, 1977; *S. bigemina* (Stiles, 1891) Levine, 1977; *Coccidium bigeminum* Stiles, 1891; *C. bigemina* var. *canis* Railliet and Lucet, 1891; *Isospora rivolta* (Stiles, 1891) Lühe, 1906; *"Isospora rivolta"* sporocysts of Gassner (1940) and *auctores* in part; "large form of *Isospora bigemina"* of Mehlhorn, Heydorn and Gestrich (1975) and Heydorn, Mehlhorn and Gestrich (1975) in part; *Lucetina bigemina* (Stiles, 1891) Henry and Leblois, 1926; *Cryptosporidium vulpis* Wetzel, 1938 (probably); *Endorimospora miescheriana* (Kühn, 1865) Tadros and Laarman, 1976.

Type Definitive Host. Dog *Canis familiaris.*

Other Definitive Hosts. Wolf *Canis lupus,* red fox *Vulpes vulpes,* raccoon *Procyon lotor.*

Type Intermediate Host. Domestic pig *Sus scrofa.*

Other Intermediate Host. Wild boar *Sus scrofa.*

Location. In pig skeletal muscle, heart, esophagus, diaphragm, and tongue (Prestwood, Cahoon and McDaniel, 1980). For other information, see Levine and Ivens (1981).

Oocyst Structure. Sporocysts in dog and raccoon 9–13 x 7–9 (mean 11 x 8) μm (Prestwood, Cahoon and McDaniel, 1980).

Merogony. There are 3 meront generations in the pig. The first-generation meronts are in the endothelial cells of the venules in the liver up to day 7 after inoculation (DAI). The second-generation meronts are in the endothelial cells of capillaries in all organs, especially the heart muscles, 8–13 or more DAI (Heydorn, Matuschka and Ipczynski, 1981). (Barrows et al. [1982] found pre-muscle meronts 17–79 x 7–11.5 μm containing 20–94 [mean 39] tachyzoites 12–13 DAI.) The sarcocysts in porcine muscle are compartmented, up to 0.5–4 mm long and up to 3 mm in diameter, with a striated wall. They contain only metrocytes at first. Bradyzoites begin to appear by

52 DAI and are the only forms present at 80 DAI; they are crescent-shaped, about 14 x 4 μm (Barrows et al., 1982).

Prepatent Period. 11–13 days in dog and raccoon (Prestwood, Cahoon and McDaniel, 1980).

Pathogenicity. Erber and Geisel (1979) found that 50,000–1 million *S. miescheriana* sporocysts caused fever and anemia followed by general hemorrhagic diathesis, coagulopathia and cardiac capillary thrombosis in pigs. Boch, Hennings and Erber (1980) said that 25,000 sporocysts did not significantly affect weight gains of pigs but did cause a transient inappetence and somnolence at the time of the second merogony; 50,000 oocysts caused significant (11–27%) weight loss.

Immunity. Erber and Geisel (1979) could not reinfect pigs with *S. miescheriana,* but found that they were still susceptible to *S. hominis.*

Remarks. Prestwood, Cahoon and McDaniel (1980) were unable to infect the cat and opossum *Didelphis marsupialis.*

***Sarcocystis suihominis* (Tadros and Laarman, 1976) Heydorn, 1977**

Synonyms. Miescheria utriculosa Harz, 1886 in part; *Sarcocystis porcihominis* Dubey, 1976; *S. suihominis* Heydorn, 1977; *Endorimospora suihominis* Tadros and Laarman, 1976.

Type Definitive Host. Man *Homo sapiens.*

Other Definitive Hosts. Chimpanzee *Chimpansee troglodytes,* rhesus monkey *Macaca mulatta,* cynomolgus monkey *M. fascicularis* (all experimental).

Type Intermediate Host. Domestic pig *Sus scrofa.*

Location. Oocysts in small intestine of man. Meronts in pig, first-generation meronts in endothelial cells of liver veins; second-generation meronts in endothelial cells of veins of all organs; sarcocysts usually in pig muscle cells but also in nerve and connective tissue cells and brain.

Oocyst Structure. Oocysts 18–20 x 12–15 (mean 19 x 13) μm (Rommel and Heydorn, 1972; Heydorn, 1977), with thin wall, without micropyle, residuum or polar granule. Sporocysts 11–14 x 8–11 μm (Rommel and Heydorn, 1972; Heydorn, 1977), without Stieda body, with residuum.

Merogony. There are 2 meront generations in the pig before sarcocyst formation. The first-generation meronts appear in the endothelial cells of the liver veins 6 days after sporocysts have been fed.

The second-generation meronts appear in the endothelial cells of the veins of all organs on days 14–17, and the sarcocysts (third-generation meronts) appear in the muscles, nerve and connective tissue cells, and brain 27 days after feeding. At 14 days, the second-generation meronts are 6–8 x 2–4 (mean 7 x 3) μm. They form a maximum of 50–90 merozoites each. These merozoites differ from those known for other coccidia. They have a 3-layered pellicle and are in the cytoplasm of the host cells, which are mainly endothelial cells of the veins and also parenchymal cells. The meront nucleus becomes giant, forms large protrusions and deep invaginations, and is very probably polyploid. Merozoites are formed simultaneously by budding. When released, they are about 6.5 x 3.2 μm. They completely destroy the host cells. In the earlier stages host cells are often found "floating" in the veins, but merozoite formation still goes on in them (Heydorn, 1977; Heydorn and Ipczynski, 1978; Heydorn and Mehlhorn, 1978; Mehlhorn and Heydorn, 1977; Tadros and Laarman, 1978).

The second-generation merozoites enter the muscle cells and become third-generation meronts (sarcocysts). They are elongate, compartmented, up to 2 x 0.5 mm, with a wall 4–9 μm thick containing cytophaneres up to 13 μm long. At first only metrocytes are present. These are globular, 9–12 x 4–6 μm. They are present up to day 142 (the last day examined). Bradyzoites are present on day 56. They are banana-shaped, 13–17 x 5–6 (mean 15 x 5) μm, and have 22 subpellicular microtubules and other typical features of *Sarcocystis* infectious stages.

Gamogony. S. suihominis can be cultivated in human skin fibroblast and intestinal cell tissue cultures, starting with bradyzoites from pig sarcocysts. Cat lung, dog kidney, and pig kidney cell cultures are not satisfactory. The bradyzoites penetrate the host cells immediately, become enclosed in a parasitophorous vacuole, begin to round up and lose their conoid, rhoptries and micronemes at 6 hours, and are recognizable as microgamonts and macrogametes 12 hours after inoculation. No meronts are formed. The microgamonts produce 20–30 triflagellate, slender microgametes about 4–5 μm long by schizogony. Development is complete 18–22 hours after inoculation; only oocysts are seen after 24 hours. Sporulation begins about 22 hours after inoculation (Mehlhorn and Heydorn, 1979; Becker, Mehlhorn and Heydorn, 1979).

Prepatent Period. 9–10 days in man (Heydorn, 1977); 12–14 days in chimpanzee and macaques (Fayer et al., 1979).

Patent Period. More than 36 days in man (Heydorn, 1977); at least 18 days (Fayer et al., 1979).

Pathogenicity. This species is pathogenic for both little pigs and man (Heydorn, 1977; Mehlhorn and Heydorn, 1977). In 2 human volunteers Heydorn (1977) reported diarrhea, nausea, vomiting, circulatory disturbance and dyspnea beginning 6–8 hours after eating raw, minced pork and lasting 36–48 hours. Piekarski et al. (1978) fed pork infected with *S. suihominis* to 8 medical students in Germany. All had acute clinical symptoms, especially diarrhea, vomiting, coldness and sweating in 6–24 hours. The symptoms decreased within 12–24 hours.

Baby pigs fed sporocysts by Heydorn (1977, 1977a) became ill with fever, dyspnea and reduced feed intake 10–13 days later. About half of the piglets fed 1–5 million oocysts died 14–17 days after inoculation, and some of them had hemorrhages all over their bodies or on their ears and tails.

Immunity. Piekarski et al. (1978) carried out serologic studies with the indirect immunofluorescence test (IIFT) 14, 43 and 71 days after inoculation on the 8 medical students they had infected with this species, using *S. gigantea* and *S. suihominis* antigens. They found a partial cross-reaction with *S. gigantea* antigen.

Fayer et al. (1979) said that prior infection did not immunize the rhesus and cynomolgus monkeys.

Cross-Transmission Studies. Heydorn (1977) was unable to infect dogs or cats by feeding muscle from baby pigs infected with sporocysts from man.

Remarks. The life cycle of this species was discovered by Rommel and Heydorn (1972).

Fayer and Leek (1979) found merozoites of this species in experimentally infected pigs and transmitted them to clean pigs by blood transfusion.

Sarcocystis porcifelis Dubey, 1976

Type Definitive Host. Domestic cat *Felis catus.*

Type Intermediate Host. Domestic pig *Sus scrofa.*

Remarks. Golobkov, Rybaltovskii and Kialyakova (1974) reported completion of the life cycle of this species. For other information see Levine and Ivens (1981).

***Sarcocystis* sp. Dubey, 1979**

Dubey (1979) found by microscopic examination after trypsin digestion that 3.5% of 286 sows in Ohio were infected with *Sarcocystis* sp. However, he was unable to transmit the organisms to dogs or cats by feeding infected porcine tissues.

***Toxoplasma gondii* (Nicolle and Manceaux, 1908) Nicolle and Manceaux, 1909**

Type Definitive Host. Domestic cat *Felis catus.*

Other Definitive Hosts. Jaguarundi *Felis yagouaroundi,* ocelot *F. pardalis,* mountain lion *F. concolor,* Asian leopard cat *F. bengalensis,* bobcat *Lynx rufus,* probably cheetah *Acinonyx jubatus.*

Type Intermediate Host. Gondi *Ctenodactylus gundi.*

Other Intermediate Hosts. Over 200 species of mammals (including felids) and birds are known. Hellmann and Tauscher (1967) found *T. gondii* in 16 of 166 samples of fresh pork, 0 of 170 samples of fresh beef, and in 30 samples of "minced meat," which probably consisted of both beef and pork, in Germany.

Pathogenesis. Hunter (1979) reported spontaneous abortion due to *T. gondii* in a herd of pigs in Canada; 5 of 25 sows aborted near term. For other information, see Levine and Ivens (1981).

Immunity. De Andrade and Weiland (1971) found cross-reactions between *Eimeria polita, E. scabra, E. nieschulzi, Isospora felis* and *T. gondii* with the micro-agar precipitation test. They found only specific reactions with the indirect fluorescent antibody and Sabin-Feldman tests using *Sarcocystis gigantea* and *T. gondii* antigens.

***Cryptosporidium muris* Tyzzer, 1907**

Cryptosporidium muris has been found in the brush border of crypt epithelial cells of the colon of domestic pigs. Kennedy, Kreitner and Strafuss (1977) saw mild inflammation of the colon in infected pigs in Kansas, but there were no clinical signs. Links (1982) said that the affected baby pigs he saw in Australia had been suffering from diarrhea.

***Adelina* sp. (Paichuk, 1953) Levine, 1977**

Synonym. Merocystis sp. Paichuk, 1953.

Type Host. Domestic pig *Sus scrofa.*

Oocyst Structure. Short-oval, mean 39 x 33 μm, with 3-layered,

smooth, very fragile wall 2 μm thick, with more than 13 spherical sporocysts 9 μm in diameter, with spherical sporozoites 4.3 μm in diameter.

Remarks. This is probably a pseudoparasite of the pig.

Host Genus *Phacochoerus*

Sarcocystis spp.

Sarcocysts of *Sarcocystis* spp. have been found in the striated muscles of the warthog *Phacochoerus aethiopicus* in Africa (Viljoen, 1921; Thils, Déom and Fagard, 1960; Sachs and Sachs, 1968; Kaliner, Grootenhuis and Protz, 1974; Kaliner et al., 1971; and Kaliner, 1975).

Host Genus *Hylochoerus*

Sarcocystis sp.

Kaliner et al. (1971) and Kaliner (1975) found sarcocysts of *Sarcocystis* sp. in striated muscles of the giant forest pig *Hylochoerus meinertzhageni* in East Africa.

Host Family CAMELIDAE

Host Genus *Camelus*

Eimeria bactriani Levine and Ivens, 1970

(Figs. 16–19, Levine and Ivens, 1970)

Synonyms. Eimeria cameli Nöller, 1933; *Eimeria cameli* Nöller, 1932 emend. Yakimoff and Matschousky, 1939 of Pellérdy, 1965; *Eimeria cameli* Iwanoff-Gobzem, 1934; ? *Eimeria nolleri* Reichenow, 1953 of Abdussalam and Rauf, 1957; [*non*] *Eimeria cameli* (Henry and Masson, 1932a) Pellérdy, 1956; [*non*] *Globidium cameli* Henry and Masson, 1932a.

Type Host. Bactrian camel *Camelus bactrianus.*

Other Host. Dromedary *Camelus dromedarius.*

Location. Small intestine, beginning about 2 m behind the pylorus and extending into the ileum.

Oocyst Structure. Spherical to ellipsoidal, about 32 x 25–27 μm,

with light yellowish to yellowish brown wall, with micropyle, without micropyle cap, without residuum. Sporocysts about 15–17 x 10 μm.

Merogony. The meronts are in the epithelial cells of the villi. They are 16 x 10 μm and contain 20–24 merozoites each 9 x 2 μm.

Gamogony. The microgamonts are also in the epithelial cells of the villi of the small intestine. They reach a diameter of 14 μm or 19 x 12 μm and contain several centers of development, each with a residual body. The mature microgametes are 4 μm long. The mature macrogametes are 25 x 20 μm and are often free in the gut lumen.

***Eimeria cameli* (Henry and Masson, 1932) Reichenow, 1952**
(Figs. 1,2,5,6–8,9–12, Levine and Ivens, 1970)

Synonyms. Globidium cameli Henry and Masson, 1932 of Enigk, 1934; *Eimeria (Globidium) cameli* (Henry and Masson, 1932) Reichenow, 1952 of Abdussalam and Rauf, 1957; *Eimeria kazachstanica* Tsygankov, 1950; *Eimeria casahstanica* [*sic*] Zigankoff, 1950 of Pellérdy, 1965; *Eimeria noelleri* (Henry and Masson, 1932) Pellérdy, 1956 of Dubey and Pande, 1964; *Eimeria iraqiensis* Mirza, 1970; [*non*] *Eimeria cameli* Nöller, 1933 of Iwanoff-Gobzem, 1934, of Yakimoff and Matschoulsky, 1939, and of Tsygankov, 1950; [*non*] *Eimeria (?) nölleri* Rastegaieff, 1930.

Type Host. Dromedary *Camelus dromedarius.*

Other Host. Bactrian camel *Camelus bactrianus.*

Location. Small intestine; cecum to a lesser extent.

Oocyst Structure. Piriform, 80–100 x 55–94 μm, with 2-layered, rough wall 12–15 μm thick, lined by a thin membrane; wall colorless at first, then becoming brown and opaque, with micropyle about 10–27 μm wide, with or without micropylar cap, without residuum, with or without polar granule. Sporocysts elongate, pointed at both ends, or ellipsoidal, 30–50 x 14.5–20 μm, without Stieda body, with residuum. Sporozoites comma-shaped, lying lengthwise head to tail in sporocysts, with clear globule at large end.

Merogony. Meronts in small intestine mucosa spherical or ellipsoidal, up to 350 μm in diameter.

Gamogony. The microgamonts are up to 350 μm in diameter and contain blastophores 20–23 μm in diameter. Microgametes about 6 μm long and 0.5 μm wide. Macrogametes in epithelial cells at the base of the glands of the ileum beginning 3 m behind the pylorus, decreasing in number posteriorly, but a few in the cecum.

***Eimeria dromedarii* Yakimoff and Matschoulsky, 1939**
(Figs. 3, 4, Levine and Ivens, 1970)

Synonyms. Eimeria cameli Nöller, 1933 of Iwanoff-Gobzem (1934) in part; *Eimeria cameli* Iwanoff-Gobzem of Tsygankov (1950) in part; ? *Eimeria cameli* Jakimov, 1934 of Ryšavý (1954).

Type Host. Dromedary *Camelus dromedarius.*

Other Host. Bactrian camel *Camelus bactrianus.*

Oocyst Structure. Ovoid, 23–33 x 20–25 (mean 28 x 23) μm, with brown, 2-layered wall 0.1–3 μm thick, thickened to form a kind of "cap" 7–8 μm wide and 2–3 μm high, without residuum or polar granule. Sporocysts ovoid or spherical, 8–11 x 6–9 μm, without Stieda body or residuum. Sporozoites comma-shaped, with 1 or 2 clear globules each.

***Eimeria pellerdyi* Prasad, 1960 emend. Pellérdy, 1965**
(Figs. 13, Levine and Ivens, 1970)

Synonym. Eimeria pellerdei Prasad, 1960.

Type Host. Bactrian camel *Camelus bactrianus.*

Oocyst Structure. Oval or ellipsoidal, 22–24 x 12–14 μm, with a smooth, colorless, 2-layered wall, without micropyle, residuum, or polar granule. Sporocysts ovoid, 9–11 x 4–6 μm, with small Stieda body and residuum. Sporozoites club-shaped, 8–10 x 1–3 μm, with central nucleus and clear globule at large end.

***Eimeria rajasthani* Dubey and Pande, 1963**
(Figs. 14,15, Levine and Ivens, 1970)

Synonym. ? Eimeria sp. Ezzat, 1961.

Type Host. Dromedary *Camelus dromedarius.*

Oocyst Structure. Nearly ellipsoidal, 34–39 x 25–27 (mode 36 x 25) μm, with 2-layered wall 2–3 μm thick, outer layer relatively thick and light yellowish green, inner layer darker, with shining inner contour, micropyle not visible but apparently present, with micropylar cap 8–11 x 2–3 μm, without residuum or polar granule. Sporocysts almost ovoid, 14–15 x 8–11 (mode 15 x 11) μm, with Stieda body and residuum. Sporozoites elongate, with one end broad and the other narrow and pointed, 10–14 x 3–4 μm, lying lengthwise head to tail in sporocysts, with 2 or sometimes more clear globules.

***Isospora orlovi* Tsygankov, 1950**
(Fig. 262, Levine and Ivens 1970)

Type Host. Camel (species not stated).

Oocyst Structure. Ellipsoidal, ovoid, piriform, cylindrical or figure–8 shaped, dark gray, 27–35 x 15–20 μm, with smooth, 2-layered wall about 1 μm thick, outer layer yellow-green or light green, inner layer rose, dark rose, red, or brown, without micropyle, residuum, or polar granule. Sporocysts ellipsoidal, ovoid, or spherical; the spherical ones 13–15 μm in diameter, the others 15–20 x 13–17 μm, without Stieda body, with residuum. Sporozoites elongate ellipsoidal, 7–10 x 4–6 μm.

Sarcocystis cameli Mason, 1910

Type Definitive Host. Dog *Canis familiaris.*

Type Intermediate Host. Camel.

Location. Sarcocysts in heart and striated muscles of intermediate host.

Oocyst Structure. Oocysts unknown. Hilali and Mohamed (1980) said that the sporocysts in dog feces average 12 x 9 μm and have a coarse residuum.

Merogony. The sarcocysts are up to 12 mm long and 2 mm wide; they are compartmented and have striated walls. The merozoites are banana-shaped, 15–20 x 4–6 μm. Metrocytes are also apparently present (Mason, 1910). Hilali and Mohamed (1980) said that the sarcocysts in the camel esophagus and diaphragm muscles are microscopic, 33–389 x 22–33 μm, and have striated walls 1–2 μm thick.

Prepatent Period. 10–14 days (Hilali and Mohamed, 1980).

Patent Period. 69–73 days (Hilali and Mohamed, 1980).

Remarks. Ghaffar et al. (1979) could not decide whether the organism they found in *C. dromedarius* in Egypt should be called *S. cameli* because they said Mason (1910) had described 2 types of cyst, one with a smooth, non-striated wall and the other with a striated wall. We think that 2 species are probably encompassed by this name, one with microscopic and the other with macroscopic sarcocysts (see below).

Sarcocystis spp.

Ippen et al. (1974) found sarcocysts of *Sarcocystis* sp. in the striated muscles of 2 of 8 *C. bactrianus* in East Germany. Ghaffar et al. (1979) found them in the striated muscles of the esophagus and diaphragm of *C. dromedarius* in Egypt. They are compartmented, 130–180 x 60–110 μm and contain both metrocytes and many merozoites. The metrocytes are 3.5–7 μm long, with a 3-membraned pellicle, rhoptries,

micronemes, amylopectin granules, a well-developed endoplasmic reticulum, micropores, and a relatively large nucleus with nucleolus. They divide by endodyogeny. The merozoites are elongate, 8–12 x 2.5–4 μm, with conoid, rhoptries, micronemes, Golgi apparatus, amylopectin granules, lipid droplets, a large, often U-shaped mitochondrion and a nucleus. The sarcocyst wall is composed of an electron-dense primary layer irregularly folded to give rise to finger-like projections 1–2 x about 0.5 μm, with knob-like elevations at their surface. The finger-like projections contain fibrils which seem to originate in the ground substance. The projections lie in direct contact with the host sarcoplasm. Under the light microscope the sarcocysts have a smooth wall with little or no striation.

Host Genus *Lama*

***Eimeria alpacae* Guerrero, 1967**
(Fig. 21, Levine and Ivens, 1970)

Oocyst Structure. Ellipsoidal, rarely ovoid, 22–26 x 18–21 (mean 24 x 20) μm, with smooth, 2-layered wall 1.2–1.6 (mean 1.45) μm thick, outer layer 1.1 μm thick, very pale greenish to bluish, inner layer 0.4 μm thick, appearing as a dark yellow line, rarely somewhat wrinkled, at micropylar end, with micropyle, with colorless to pale greenish micropylar cap 0.7–1.3 μm high and 4.4–7.5 μm wide (mean 1.0 x 5.7 μm), with or without polar granule, without residuum. Sporocysts ovoid, 10–13 x 7–8 (mean 11 x 7) μm, with wall about 0.2 μm thick, with very faintly perceptible Stieda body, with residuum. Sporozoites elongate, with one end narrower than the other, lying lengthwise head to tail in sporocysts, with 1–3 clear globules.

***Eimeria lamae* Guerrero, 1967**
(Fig. 20, Levine and Ivens, 1970)

Type Host. Alpaca *Lama pacos.*

Oocyst Structure. Ellipsoidal, occasionally ovoid, slightly flattened at micropylar end, which is sometimes the smaller one, 30–40 x 21–30 (mean 36 x 24.5) μm, with smooth, 2-layered wall 1.4–1.8 (mean 1.7) μm thick, outer layer 1.3 μm thick, bluish to greenish yellow, inner layer 0.5 μm thick, brownish-yellow, sometimes somewhat wrinkled at micropylar end, with micropyle, with prominent, dome-

shaped, colorless to light grayish micropylar cap 1.5–2.2 μm high and 9–11 μm wide (mean 1.8 x 10 μm), with or without polar granule, without residuum. Sporocysts elongate ovoid, 13–16 x 8–10 (mean 15 x 8.5) μm, with wall about 0.25 μm thick, with Stieda body and residuum. Sporozoites elongate, with one end narrower than the other, lying lengthwise head to tail in sporocysts, with 1–3 clear globules.

***Eimeria macusaniensis* Guerrero, Hernandez, Bazalar and Alva, 1971**

(Fig. 309)

Synonym. Eimeria sp. Guerrero, Hernandez and Alva, 1967.

Type Host. Alpaca *Lama pacos.*

Oocyst Structure. Ovoid, sometimes piriform, 81–107 x 61–80 (mean 94 x 67) μm with 3-layered wall 8–11 (mean 9) μm thick, outer layer smooth, colorless, 1 μm thick, middle layer granular, dark brown, 7.5 μm thick, inner layer colorless, 1 μm thick, with micropyle, with dome-shaped, colorless to light greenish micropylar cap 2–5 μm high and 9–14 μm wide (mean 3 x 12 μm), without residuum or polar granule. Sporocysts elongate ovoid, 33–40 x 16–20 (mean 36 x 18) μm, with faintly perceptible Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with a large clear globule at the large end and usually a small one at the small end.

***Eimeria peruviana* Yakimoff, 1934**

(Fig. 31, Levine and Ivens, 1970)

Type Host. Llama *Lama glama.*

Oocyst Structure. Ellipsoidal, 28–38 x 18–23 (mean 32 x 19) μm, with double-membraned wall, without micropyle or polar granule, with residuum. Sporocysts more or less ellipsoidal, 10–15 x 7.5 μm, without Stieda body. Sporozoites elongate, lying lengthwise in sporocysts.

***Eimeria punoensis* Guerrero, 1967**

(Fig. 22, Levine and Ivens, 1970)

Type Host. Alpaca *Lama pacos.*

Oocyst Structure. Ellipsoidal, occasionally ovoid, 17–22 x 14–18 (mean 20 x 16) μm, with smooth, 2-layered wall 0.8–1.1 (mean 1.0)

μm thick, outer layer blue to purplish, 0.7 μm thick, inner layer 0.3 μm thick, appearing as a dark line, with micropyle, with flat, colorless micropylar cap 0.4–0.8 μm high and 3.5–5.5 μm wide (mean 0.5 x 4.1 μm), sometimes difficult to see, with or without polar granule, without residuum. Sporocysts somewhat elongate ovoid, 8–11 x 5–7 (mean 9 x 6) μm, with faintly perceptible Stieda body, with residuum. Sporozoites elongate, with one end narrower than the other, lying lengthwise head to tail in sporocysts, with 1–3 clear globules.

***Sarcocystis aucheniae* Brumpt, 1913**

Type Definitive Host. Unknown.

Type Intermediate Host. Llama *Lama glama.*

Location. Sarcocysts in striated muscles.

***Sarcocystis* sp.**

Guerrero, Hernandez and Alva (1967) found sarcocysts of *Sarcocystis* sp. in the striated muscles of *L. pacos* in Peru, and Ippen et al. (1974) found them in 1 of 6 *L. pacos* in East Germany.

Host Family TRAGULIDAE

Host Genus *Tragulus*

***Eimeria kanchili* Mullin and Colley, 1971** (Fig. 313)

Type Host. Lesser mouse-deer *Tragulus javanicus.*

Oocyst Structure. Subspherical to spherical, 9–13 x 9–13 (mean 11 x 11) μm, with smooth, 1-layered yellowish brown wall about 1 μm thick, without micropyle or residuum, with 1–2 polar granules. Sporocysts ellipsoidal, 8–11 x 3–6 (mean 9 x 5) μm, with small Stieda body and residuum. Sporozoites comma-shaped, lying lengthwise head to tail in sporocysts, with clear globule at large end.

***Eimeria pelandoki* Mullin and Colley, 1971** (Fig. 316)

Type Host. Lesser mouse-deer *Tragulus javanicus.*

Oocyst Structure. Subspherical to spherical, 15–21 x 15–21 (mean 18 x 17) μm, with 2-layered, rough, striated wall, outer layer pale

yellow, 1 μm thick, inner layer pale yellow, 0.75 μm thick, without micropyle or residuum, with polar granule. Sporocysts ellipsoidal, 10–13 x 4–8 (mean 12 x 6) μm, with small Stieda body and residuum. Sporozoites stout, comma-shaped, lying lengthwise head to tail in sporocysts, with clear globule at broad end.

***Eimeria ramgai* Pande, Bhatia, Chauhan and Garg, 1970** (Fig. 303)

Type Host. Mouse deer *Tragulus meminna.*

Oocyst Structure. Ovoid, 17–24 x 14–20 (mean 20 x 17) μm, with 2-layered wall 1–1.5 μm thick, outer layer light yellowish, inner layer brown, without micropyle, residuum or polar granule. Sporocysts ovoid, 10–13 x 4–5 (mean 11 x 4.5) μm, without Stieda body, with residuum. Sporozoites 2.4 x 1 μm, with one end broadly rounded and the other tapering, with clear globules at both ends and small central nucleus.

Oocyst Structure. Ellipsoidal to subspherical, 20–30 x 18–25 (mean 26 x 23) μm, with smooth, 2-layered wall, outer layer blue-gray, about 0.75 μm thick, inner layer yellowish brown, about 0.75 μm thick, without micropyle or residuum, with polar granule. Sporocysts ellipsoidal, 17–20 x 9–11 (mean 18 x 10) μm, with prominent Stieda body and residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with large clear globule at broad end and small one usually at narrow end. Excysted living sporozoites vermiform, 16 x 5 μm, with one end narrow and pointed and the other end rounded, with a relatively large clear globule near the posterior end and a smaller one anterior to the nucleus (Colley and Mullin, 1972).

Host Family CERVIDAE

Host Genus *Muntiacus*

***Eimeria dawari* Bhatia, Chauhan, Arora and Agrawal, 1973** (Fig. 328)

Type Host. Barking deer *Muntiacus muntijak.*

Oocyst Structure. Subspherical to ovoid, 21–23 x 19–20 (mean 22 x 20) μm, with "double-contoured" wall, outer layer light yellowish green, inner layer dark yellowish brown, without micropyle or resid-

uum, with numerous polar granules. Sporocysts broadly ovoid, 11–12 x 7–8 (mean 11 x 7) μm, with small, knob-like Stieda body and a few residual granules. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 1 clear globule at each end.

***Eimeria sardari* Bhatia, Chauhan, Arora and Agrawal, 1973** (Fig. 329)

Type Host. Barking deer *Muntiacus muntijak.*

Oocyst Structure. Elongate ellipsoidal, 28–31 x 13–15 (mean 29 x 14) μm, with 2-layered wall 1.5 μm thick, outer layer yellowish green, inner layer yellowish brown, without micropyle, residuum or polar granule. Sporocysts essentially ellipsoidal, 11–12 x 7–8 (mean 11 x 7) μm, with vestigial Stieda body and few scattered residual granules. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with a clear globule at each end.

Host Genus *Dama*

***Eimeria* spp. Ryšavý, 1954**

Synonyms. Eimeria arloingi Marotel, 1905 of Ryšavý, 1954 in *Dama dama; E. crandallis* Honess, 1942 of Ryšavý, 1954 in *Dama dama; E. faurei* Moussu and Marotel, 1901 of Ryšavý, 1954 in *Dama dama; E. intricata* Spiegl, 1925 of Ryšavý, 1954 in *Dama dama; E. ninae-kohl-yakimovi* Yakimoff and Rastegaieva, 1930 of Ryšavý, 1954 in *Dama dama; E. parva* Kotlan, Moczy and Vajda, 1929 of Ryšavý, 1954 in *Dama dama.*

Type Host. Fallow deer *Dama dama.*

Remarks. Ryšavý (1954) reported the above 6 species of *Eimeria* as occurring in *Dama dama* in Czechoslovakia. He did not describe any of them and he attempted no cross-transmission experiments. It is extremely doubtful that they actually belonged to the species to which he assigned them.

***Sarcocystis* sp.**

Sarcocystis sp. has been reported in the striated muscles of fallow deer *Dama dama* in England, Czechoslovakia and Hungary by Brooks (1903), Ippen et al. (1974), Blažek, Kotrly and Ippen (1976) and Kavai and Sugar (1976).

Host Genus *Axis*

***Eimeria cervis* Mandal and Choudhury, 1982**

Type Host. Spotted deer *Axis axis.*

Location. Feces.

Oocyst Structure. Subspherical, 13–15 x 10–12 (mean 14 x 11) μm, with a 2-layered wall, the outer layer thin and the inner layer 0.8–1 μm thick, without a micropyle, usually without a residuum, apparently without polar granules. Sporocysts cylindrical, slightly curved, with one end narrower than the other, 7–8 x 2–3 μm, without residuum, illustrated without a Stieda body. Sporozoites elongate, club-shaped, with tapered anterior end and blunt posterior end, with a clear globule at the large end, lying lengthwise head to tail in the sporocysts, 3–6 x 1–2 (mean 5 x 1) μm. Sporulation time 2–3 days at 28–30 C in 2.5% potassium bichromate solution.

***Eimeria cheetali* Bhatia, 1968** (Figs. 324–327)

Type Host. Spotted deer *Axis axis.*

Oocyst Structure. Ellipsoidal, 24–31 x 14–16 (mean 26 x 15) μm, with 2-layered wall 1–1.3 μm thick, outer layer yellowish green, inner layer dark brown, with micropyle 2.0–2.6 μm in diameter, without residuum or polar granule. Sporocysts ovoid, 9–12 x 5–7 (mean 12 x 6.5) μm, without Stieda body, with residuum composed of scattered granules. Sporozoites banana-shaped, with one end broader than the other, lying lengthwise head to tail in sporocysts, with large clear globule at broad end and small one at narrow end.

Remarks. Bhatia (1968) said that this species also occurred in the black buck *Antilope cervicapra,* but that its oocysts and sporocysts were smaller in that host. However, it is extremely doubtful that it occurs in both *Axis* and *Antilope,* because they are not only different genera but belong to different families.

***Eimeria parahi* Pande, Bhatia, Chauhan and Garg, 1970** (Fig. 297)

Type Host. Hog deer *Axis porcinus.*

Oocyst Structure. Subspherical, 16–20 x 13–15 (mean 18 x 14) μm, with 2-layered wall, outer layer straw-colored, 1.3 μm thick, inner layer yellowish brown, with micropyle represented by a thinning of the wall at one end, without residuum or polar granule. Sporocysts

ellipsoidal, presumably 9–10 x 4–5 μm, with minute Stieda body, with residuum. Sporozoites elongate oval, 6–8 x 2 μm, with one end broad and the other pointed, with a small central nucleus and a large clear globule at the broad end.

***Eimeria wassilewskyi* Rastegaieff, 1930**

(Fig. 24, Levine and Ivens 1970)

Synonyms. Eimeria wassilewsky Rastegaieff, 1930 *lapsus calami; E. wassilewsky* Rastegaieff of Yakimoff and Sokoloff (1935) (*lapsus calami*) in part; *E. wasielewskyi* Rastegaieff of Pellérdy (1963) *lapsus calami;* [*non*] *E. wassilewsky* [*sic*] Rastegaieff of Yakimoff and Sokoloff (1935) in *Cervus elaphus* and *Cervus* (syn., *Sika) hortulorum.*

Type Host. Axis deer *Axis axis.*

Oocyst Structure. Ovoid, 18 x 14 μm, with a micropyle 4.5 μm in diameter (Rastegaieff, 1930). Ovoid, 17–20 x 13–16 (mean 18.5 x 14) μm, with a 2-layered wall 0.75–1.0 μm thick, the outer layer yellowish and thinner than the inner layer, with a micropyle 3.5–4.5 μm in diameter, with a residuum (which appears in their drawing to be a number of polar granules). Sporocysts ovoid, with Stieda body and residuum, 8–11 x 3–6 (mean 9 x 4.5) μm. Sporozoites elongate, tapering at anterior end and rounded at posterior, 7–8 x 2–3 (mean 7.5 x 2.5) μm, lying lengthwise head to tail in sporocysts, with clear globule at broad end (Mandal and Nair, 1974).

***Eimeria* sp. Bhatia, 1968**

Type Host. Spotted deer *Axis axis.*

Oocyst Structure. Ovoid, 40 x 25 μm, with smooth, 2-layered wall, outer layer yellowish green 1 μm thick, inner layer brownish, 0.6 μm thick, with micropyle 1 μm in diameter, without residuum or polar granule. Sporocysts spindle-shaped, 16–17 x 8–9 μm. The oocysts did not sporulate completely in 3 days.

***Eimeria* (?) sp. (Rastegaieff, 1930) Levine and Ivens, 1970**

Synonym. Coccidium sp. Rastegaieff, 1930.

Type Host. Axis deer *Axis axis.*

Oocyst Structure. Ovoid, with one end flattened, 18 x 14 μm, with a micropyle 4.5 μm in diameter. Sporulated oocysts not described.

Host Genus *Cervus*

***Eimeria asymmetrica* Supperer and Kutzer, 1961**
(Figs. 25–28, Levine and Ivens, 1970)

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Slightly ovoid, partially asymmetrical with one side a little flatter than the other, 25–33 x 15–18 μm, with colorless to yellowish wall, illustrated as smooth and 1-layered, with micropyle, without residuum or polar granule. Sporocysts ovoid, 8–10 x 6–7 μm, without Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 1–2 clear globules.

***Eimeria austriaca* Supperer and Kutzer, 1961**
(Figs. 23,63, Levine and Ivens, 1970)

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Ellipsoidal to broadly ovoid, 17–25 x 14–20 μm, with thin, smooth, colorless wall illustrated as 1-layered, without micropyle, residuum or polar granule. Sporocysts spindle-shaped, 10–13 x 5–6 μm, illustrated without Stieda body, without residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 1 or more clear globules.

Cross-Transmission Studies. Supperer and Kutzer (1961) could not transmit this species to the ox, sheep or goat.

***Eimeria cervi* Galli-Valerio, 1927**

Synonym. [*non*] *Eimeria cervi* Galli-Valerio of Boch and Lucke (1961)

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Piriform, slightly flattened at micropylar end, 33 x 21 μm, with poorly visible micropyle. Sporocysts ovoid, 12 x 9 μm. Sporozoites comma-shaped, 3 x 2 μm.

***Eimeria elaphi* Jansen and van Haaften, 1966**
(Fig. 38, Levine and Ivens, 1970)

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Spherical or subspherical, 10–15 x 9–13 (mean 13 x 12) μm, with smooth wall (illustrated as 1-layered), without micropyle, residuum or polar granule. Sporocysts 6–10 x 2–4 (mean 8

x 3) μm, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts.

***Eimeria gallivalerioi* Rastegaieff, 1930**

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Ovoid, 16–23 x 11–14 μm. Rastegaieff (1930) said that the oocysts did not sporulate, but she nevertheless indicated in her table that there was no oocyst residuum and that the sporocysts were piriform. She gave no further description.

***Eimeria hegneri* Rastegaieff, 1930**

Type Host. Wapiti *Cervus elaphus* (syn., *C. canadensis).*

Oocyst Structure. Ovoid, flattened at the small end, 16–18 x 11–14 μm, with micropyle 3.6 μm in diameter. This form apparently did not sporulate. No further description given.

***Eimeria robusta* Supperer and Kutzer, 1961**

(Figs. 29,30,35,36, Levine and Ivens, 1970)

Synonym. Eimeria cervi Galli-Valerio of Boch and Lucke, 1961.

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Ovoid, 31–43 x 22–31 μm (Supperer and Kutzer, 1961), with 2-layered wall 2–3 μm thick, outer layer brown, rough, with granular surface, easily separated from smooth, colorless to yellowish inner layer after incubation in 1.5% potassium bichromate solution; inner layer about 1 μm thick, often slightly flattened at small end, with micropyle and polar granule, without residuum. Sporocysts elongate ovoid, 14–19 x 7–10 μm, with residuum, illustrated without Stieda body. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 2 clear globules each.

Cross-Transmission Studies. Supperer and Kutzer (1961) were unable to transmit this species to the ox, sheep, or goat.

***Eimeria schoenbuchi* Boch, 1963**

(Figs. 32,34, Levine and Ivens, 1970)

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Almost spherical, 53–62 (mean 59) μm in diameter, with brownish, 2-layered wall 3.0–4.5 μm thick, with wavy, sticky surface, without micropyle or apparently polar granule, with residuum. Sporocysts elongate ovoid, later spindle-shaped, 26–28 μm

long. Sporozoites granular, lying lengthwise head to tail in sporocysts, with clear globules near center and at large end.

***Eimeria sordida* Supperer and Kutzer, 1961**
(Fig. 37, Levine and Ivens, 1970)

Type Host. Red deer *Cervus elaphus.*

Oocyst Structure. Ellipsoidal to ovoid, 30–34 x 21–25 μm, with thick, yellowish to yellowish brown, often rather rough, possibly 1-layered wall, almost always with fecal particles adhering to it, with micropyle, micropylar cap and polar granule, without residuum. Sporocysts elongate ovoid, 12–13 x 7.5 μm, with residuum.

***Eimeria wapiti* Honess, 1955**
(Fig. 41, Levine and Ivens, 1970)

Type Host. Elk *Cervus elaphus* (syn., *C. canadensis nelsoni).*

Oocyst Structure. Ovoid, 32–42 x 24–29 (mean 38 x 26) μm, with light yellowish brown wall 1.5–2 μm thick, with outer surface pitted with small craters, with micropyle about 4 μm in diameter, without residuum. Sporocysts boat-shaped, pointed at one end and somewhat rounded at the other, 20 x 9.5 μm, without residuum.

***Sarcocystis cervi* Destombes, 1957**

Type Definitive Host. Unknown.

Type Intermediate Host. Deer (scientific name not given).

Merogony. Sarcocysts in striated muscles, not described, but said to resemble those in the pig and mouse.

Remarks. The only species of *Cervus* in Vietnam are the samber *C. unicolor* and thamin or Elds' deer *C. eldi* (Ellerman and Morrison-Scott, 1951). Presumably Destombes (1957) found his *S. cervi* in one of these.

***Sarcocystis cervicanis* Hernandez, Navarete, and Martinez, 1981**

Synonym. Sarcocystis sp. Navarete, Hernandez, Calero and Martinez, 1978.

Type Definitive Host. Dog *Canis familiaris.*

Type Intermediate Host. Red deer *Cervus elaphus.*

Location. Sarcocysts in deer striated muscles; oocysts and sporocysts in dog small intestine.

Merogony. Sarcocysts 150–170 x 40–50 μm in heart muscles, with

a primary wall 32 nm wide and amorphous ground substance 0.25 μm thick forming wall 0.2–0.4 μm thick, with a few hairlike protrusions 1.4 μm long and 32 nm wide on the primary wall. Metrocytes unknown. Bradyzoite mean dimensions 13 x 3 μm, with 4 rhoptries, 2 preconoidal rings, 550–650 micronemes and 22 subpellicular microtubules (Hernandez et al., 1981).

Sporogony. Sporocysts in dog feces ellipsoidal, 15–17 x 10–12 (mean 16 x 11) μm, with Stieda body, without residuum (Navarrete et al., 1978).

Prepatent Period. 11 days in dog.

Patent Period. 18 days.

***Sarcocystis sybillensis* Dubey, Jolley and Thorne, 1983**

Type Definitive Host. Dog (experimental).

Type Intermediate Host. North American elk *Cervus elaphus.*

Location. Sarcocysts in elk muscles; oocysts and sporocysts in dog small intestine.

Merogony. Sarcocysts microscopic, 506 x 29 μm, compartmented, with wall up to 8 μm thick, with hairy projections in the wall. Metrocytes 9 x 5 μm. Bradyzoites 11 x 3 μm.

Sporogony. Oocysts in dog intestine 21 x 16 μm. Sporocysts ellipsoidal, 14 x 11 μm, without Stieda body, with residuum. Sporozoites 10.5 x 3 μm.

Prepatent Period. 13 days in dog.

***Sarcocystis wapiti* Speer and Dubey, 1982**

Synonym. Sarcocystis sp. Margolin and Jolley, 1979 (?).

Type Definitive Host. Dog *Canis familiaris.*

Other Definitive Host. Coyote *Canis latrans.*

Type Intermediate Host. Wapiti *Cervus elaphus.*

Location. Sarcocysts in wapiti muscles; oocysts and sporocysts in dog and coyote small intestine.

Merogony. Sarcocysts compartmented, 652 x 322 μm, with thin primary wall. Metrocytes 11 x 5 μm. Bradyzoites 16 x 2 μm.

Sporogony. Oocysts in dog intestine 20 x 16 μm. Sporocysts ellipsoidal, 16 x 11 μm, without Stieda body, with residuum.

Prepatent Period. 9 days in dog and coyote (Speer and Dubey, 1982).

Cross-Transmission Studies. Speer and Dubey (1982) could not infect the cat with this species.

***Sarcocystis* spp.**

Synonym. Sarcocystis cervi von Hessling, 1854 of Holz (1953) and Drost (1977).

Sarcocysts of *Sarcocystis* spp. have been reported in the muscles of *C. elaphus* with little or no description in various parts of the world (Collins, Charleston and Wiens, 1980; von Hessling, 1854; Holz, 1953; Ippen et al., 1974; Drost and Graubmann, 1975; Blažek, Kotrly and Ippen, 1976; Kavai and Sugar, 1976; Drost, 1977; Pond and Speer, 1979; Mahrt and Colwell, 1980; Margolin and Jolley, 1979; Brooks, 1901; B. Schwartz, 1928; J. E. Schwartz, 1942; Sayama, 1952; Honess and Winter, 1956; and Keem, 1974).

Fayer, Dubey and Leek (1982) fed 3 calves sporocysts (from the coyote) of *Sarcocystis* sp. originally from the elk. The calves remained healthy, but one had intramuscular sarcocysts, suggesting to them either low infectivity of cattle by these forms or spurious natural infection.

Yakimoff and Sokoloff (1934) found a *Sarcocystis* in the maral *Cervus canadensis asiaticus* which they thought was the same as the form in the reindeer; they named both *S. grueneri.* However, we think it exceedingly dubious that the same species of *Sarcocystis* would occur in both these hosts, and we are confining the name *S. grueneri* to the reindeer species.

***Sarcocystis* sp. Ippen et al., 1974**

Type Definitive Host. Unknown.

Type Intermediate Host. Sika deer *Cervus nippon.*

Host Genus *Cervulus*

***Sarcocystis* sp.**

Definitive Host. Unknown.

Type Intermediate Host. Deer *Cervulus* sp. (?).

Remarks. This form was reported from the striated muscles of a "cerro" in Sumatra by Jongh (1913). Babudieri (1932) said that *Cervus* does not exist on Sumatra, so he thought it might be *Cervulus,* but this name is not included in Walker et al. (1975).

Host Genus *Odocoileus*

***Eimeria ivensae* Todd and O'Gara, 1970**
(Fig. 290, Levine and Ivens, 1970)

Type Host. Mule deer *Odocoileus h. hemionus.*

Oocyst Structure. Ovoid to slightly piriform, flat at narrow end, 30–37 x 18–22 (mean 32.5 x 21) μm with rough, 2-layered wall about 1.5 μm thick, outer layer brown, about ¾ of the wall thickness, inner layer light blue, with micropyle 4–5 μm in diameter at narrow end of oocyst, with polar granule, without residuum. Sporocysts elongate ovoid, 14–18 x 6–9 (mean 16 x 7) μm, with or without minute Stieda body, with residuum. Sporozoites lie lengthwise head to tail in sporocysts, with clear globule at each end.

***Eimeria madisonensis* Anderson and Samuel, 1969**
(Fig. 289, Levine and Ivens, 1970)

Type Host. White-tailed deer *Odocoileus virginianus.*

Other Host. Mule deer *Odocoileus h. hemionus.*

Oocyst Structure. Spherical or subspherical, 14–19 x 13–16 (mean 16 x 15.5) μm, with smooth, pale yellow, 2-layered wall, without micropyle, residuum or polar granule. Sporocysts ellipsoidal, 6–9 x 4–6 (mean 7.5 x 4.5) μm, with thin wall and prominent Stieda body, without residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with small clear globule at broad end.

Prepatent Period. 18 days in an experimentally infected mule deer fawn (Abbas and Post, 1980).

Patent Period. 10 days in an experimentally infected mule deer fawn (Abbas and Post, 1980).

***Eimeria mccordocki* Honess, 1941**
(Figs. 62, 286, Levine and Ivens, 1970)

Type Host. Mule deer *Odocoileus h. hemionus.*

Other Host. White-tailed deer *Odocoileus virginianus.*

Location. Posterior ileum, above the host cell nuclei of the villar epithelial cells, but not in the crypts of Lieberkuehn.

Oocyst Structure. Ellipsoidal, 33–37 x 25–29 (mean 35 x 27) μm, with 2-layered wall 1.1 μm thick, outer layer smooth, deep yellowish brown, inner layer not described, with micropyle 5–6 μm in diame-

ter, without residuum. Sporocysts oblong, with one end pointed and the other bluntly rounded, 18–21 x 8–12 μm, with Stieda body and residuum (Landram and Honess, 1955).

Merogony. There are 2 asexual generations. First-generation meronts are mature at 9 days. They are 9–13 x 8–10.5 μm and contain a small residuum and 8–22 banana-shaped merozoites 6 x 2 μm with one end rounded and the other pointed, and with an eosinophilic globule at each end. Second-generation meronts are 10–14 x 9.5–13.5 μm and contain 13–28 merozoites 7–7.5 x 2 (mean 7 x 2) μm (Abbas and Post, 1980; Abbas, Post and Marquardt, 1983).

Gamogony. According to Abbas and Post (1980) and Abbas, Post and Marquardt (1983), these occur in the same location as the meronts. The macrogametes are 3.5–25 μm in diameter and the microgamonts are 9.5–15.5 μm in diameter.

Prepatent Period. 15 days in an experimentally infected mule deer fawn (Abbas and Post, 1980).

Patent Period. 12 days in an experimentally infected mule deer (Abbas and Post, 1980).

Pathogenicity. Abbas and Post (1980) found that this species caused diarrhea and increased body temperature in mule deer fawns beginning 8–9 days after experimental inoculation. Dehydration and limited emaciation were also present and flecks of blood were seen in the diarrheic feces after inoculation. Recovery followed. They thought that both the meronts and gamonts were pathogenic.

***Eimeria odocoilei* Levine, Ivens and Senger, 1967**
(Figs. 39, 288, Levine and Ivens, 1970)

Type Host. Mule deer *Odocoileus h. hemionus.*

Other Host. White-tailed deer *Odocoileus virginianus.*

Location. Posterior small intestine.

Oocyst Structure. Subspherical, 26–28 x 22–26 (mean 27 x 23.5) μm, with smooth, l-layered wall about 1.3 μm thick (confirmed by breaking the wall), outer ⅔ of wall colorless, inner ⅓ brownish yellow, giving the illusion of 2 layers, without micropyle or residuum, with polar granule. Sporocysts ovoid, 13–15 x 8–10 (mean 14 x 9) μm, with Stieda body at small end, with residuum. Sporozoites broadly comma-shaped, lying lengthwise head to tail in sporocysts, with clear globule at broad end; sporozoites sausage-shaped after emergence from sporocysts.

***Eimeria virginianus* Anderson and Samuel, 1969**
(Fig. 287, Levine and Ivens, 1970)

Type Host. White-tailed deer *Odocoileus virginianus.*

Oocyst Structure. Elongate ovoid to ellipsoidal, 42–55 x 26–42 (mean 49 x 33) μm, with rough, 2-layered wall, outer layer yellow-brown, 3 μm thick, inner layer less than 1 μm thick, with micropyle 3–6 μm in diameter, without residuum or polar body. Sporocysts ellipsoidal, pointed at one end, 19–27 x 8–11 (mean 24 x 10) μm, with thin wall and Stieda body, apparently without residuum. Sporozoites banana-shaped, rounded at both ends, lying lengthwise in sporocysts, usually with 4 large clear globules.

***Cryptosporidium* sp.**

Dubey, Kistner and Callis (1983) found *Cryptosporidium* sp. in the brush border of the small intestine epithelial cells in an *O. hemionus* fawn in Montana. They did not describe it. It was probably *C. muris.*

***Sarcocystis hemionilatrantis* Hudkins and Kistner, 1977**

Type Definitive Host. Coyote *Canis latrans.*

Other Definitive Host. Dog *Canis familiaris.*

Type Intermediate Host. Mule deer *Odocoileus hemionus.*

Location. Sexual stages in small intestine of *Canis;* sarcocysts in striated muscles of *O. hemionis;* earlier meronts in macrophages, between muscle fibers and near blood vessels in muscle tissues of *O. hemionis.*

Oocyst Structure. Sporulated oocysts 19–22 x 16-19 (mean 21 x 17.5) μm, ellipsoidal, with a thin wall, without micropyle, polar granule or residuum (Speer, Pond and Ernst, 1980). Sporocysts 14–16 (mean 14 x 9) μm in coyote and 14–16 x 9 (mean 14.5 x 9) μm in dog, without Stieda body, with residuum (Hudkins-Vivion, Kistner and Fayer, 1976). The sporocysts seen by Speer, Pond and Ernst (1980) in the coyote were 15–17 x 9–12 (mean 16 x 10) μm, ellipsoidal, without a Stieda body, with a residuum. Those seen by Arther and Post (1977) in coyotes in Colorado were 14–17 x 8–11 (mean 16 x 10) μm.

Merogony. Hudkins-Vivion, Kistner and Fayer (1976) saw microscopic meronts in the macrophages, between muscle fibers and near blood vessels in the esophagus, heart, biceps femoris, semimembranosus, diaphragm and tongue of fawns that died 27–39 days after

inoculation. The sarcocysts are apparently macroscopic and occur in the striated muscles. Hudkins and Kistner (1977) did not find them until 60 days after inoculation.

Dubey, Kistner and Callis (1983) described merogony in mule deer fed sporocysts from the dog and coyote. There are 4 generations of meront. First-generation meronts are in the arteries and capillaries of the lung 14 days after inoculation (DAI); they are 26.5 x 20 μm and contain over 100 merozoites each. First- and second-generation meronts are in the kidney, thyroid gland, hepatic lymph node, mesenteric lymph nodes and spinal cord 24 DAI. Second-generation meronts are in capillaries in the lung, spleen, brain, lymph nodes, kidney and adrenal gland 29–40 DAI; they are 20.5 x 13.5 μm and contain 20–35 merozoites. Third-generation meronts are in macrophages in the tongue, heart, esophagus, diaphragm and limb muscles 24–40 DAI; they are 20 x 14 μm and contain 10–60 merozoites. Sarcocysts up to 525 x 36 μm are in the skeletal muscles 63–90 DAI. At first they contain only metrocytes, but by day 90 they contain only bradyzoites. They are compartmented and have a smooth, thin, cross-striated wall 1–2 μm thick.

Gamogony. Speer, Pond and Ernst (1980) described gamogony in the coyote. It occurs in the lamina propria of the villi of the distal duodenum and all of the jejunum and ileum. They saw no meronts or gamonts, but they did not examine the coyotes earlier than 3 days after inoculation. They found only zygotes and developing oocysts.

Prepatent Period. 11 or more days (Hudkins and Kistner, 1977); 9-13 days in the coyote (Speer, Pond and Ernst, 1980).

Patent Period. 12–36 days (Hudkins and Kistner, 1977); 31–35 days in the coyote (Speer, Pond and Ernst, 1980).

Pathogenicity. This species is pathogenic for mule deer fawns. Nine of 11 mule deer fawns infected by Hudkins and Kistner (1977) died 27–63 days after inoculation, with anorexia, weight loss, fever and weakness. Koller, Kistner and Hudkins (1977) said that the fawns developed clinical signs 18 days after infection with sporocysts from coyotes. Early lesions in skeletal muscle consisted of perivascular necrosis with mononuclear and neutrophil infiltration, plus edema, degeneration and focal necrosis of the muscle. This reaction subsided and the cellular infiltrate dissipated. An infected macrophage usually remained, being surrounded by a clear halo. The *Sarcocystis* meronts developed in the macrophage cytoplasm, and the cytoplasmic membrane eventually ruptured, releasing merozoites.

Speer, Pond and Ernst (1980) saw no obvious clinical signs in infected coyote pups, but there was a pronounced cellular reaction in one 14 days after primary infection and in 3 others 3–7 days after a second feeding 16–17 days after the first one.

Immunity. Speer, Pond and Ernst (1980) found no evidence that immunity had developed in coyote puppies fed 16–17 days after a primary feeding.

Cross-Transmission Studies. Hudkins and Kistner (1977) were unable to infect a calf *Bos taurus* or 2 lambs *Ovis aries* with sporocysts from the coyote.

Remarks. Emnett and Hugghins (1982) found sarcocysts of what they considered to be *Sarcocystis hemionilatrantis* in the tongues of 44% of 127 white-tailed deer *Odocoileus virginianus* and 80% of 99 mule deer *O. hemionus* in South Dakota. They looked alike. Both produced sporulated sporocysts in the coyote, dog and gray fox *Urocyon cinereoargentus* but not in the red fox, raccoon or bobcat *Felis rufus.* The prepatent periods of the white-tailed deer form were 8 days in the coyote, 8–11 days in the dog and 10 days in the gray fox; those of the mule deer form were 7–8 days in the coyote and dog, and 8 days in the gray fox. The patent period of the white-tailed deer form was more than 57 days in the coyote and dog, and more than 50 days in the gray fox. The patent period of the mule deer form was more than 63 days in the coyote and dog, and more than 52 days in the gray fox (the animals were no longer examined after these times).

***Sarcocystis odocoileocanis* Crum, Fayer and Prestwood, 1981**

Type Definitive Host. Dog *Canis familiaris.*

Type Intermediate Host. White-tailed deer *Odocoileus virginianus.*

Other Intermediate Hosts. Ox *Bos taurus* and sheep *Ovis aries,* but with low infectivity for these animals.

Location. Sporocysts in dog feces; sarcocysts in intermediate host skeletal and heart muscles.

Oocyst Structure. Oocysts not described. Sporocysts ellipsoidal, 13–16 x 9–12 (mean 15 x 11) μm, with residuum, without Stieda body.

Merogony. Only sarcocysts known. Those in the skeletal muscles of white-tailed deer 104 days after inoculation were 149–536 x 29–51 (mean 264 x 40) μm. Some sarcocysts in experimentally infected deer had thin, smooth walls and others had thick, striated ones (based on their illustrations).

Prepatent Period. 7–15 (mean 10.6) days.

Patent Period. 4 to at least 30 days.

Pathogenicity. Apparently insignificant.

Remarks. Crum, Fayer and Prestwood (1981) transmitted this species from the white-tailed deer to the dog and from it to white-tailed deer, cattle and sheep. They differentiated it from *S. hemionilatrantis, S. tenella and S. cruzi* because it (1) has low infectivity for calves and sheep, and (2) has apparent insignificant pathogenicity for its intermediate host.

Sarcocystis odoi Dubey and Lozier, 1983

Type Definitive Host. Cat *Felis catus.*

Type Intermediate Host. White-tailed deer *Odocoileus virginianus.*

Location. Sporocysts in cat small intestine; sarcocysts in intermediate host skeletal muscles.

Oocyst Structure. Sporulated oocysts from intestinal scrapings of cat 16–21 x 12.5–16 (mean 18 x 14) μm, without residuum or polar granule. Sporulated sporocysts in intestinal scrapings ellipsoidal, 11–15 x 9–11 (mean 13 x 10) μm, without Stieda body, with residuum. Sporocysts in cat feces 11–13 x 7–11 (mean 12 x 9) μm. Sporozoites 8 x 1.5 μm, lying lengthwise in sporocysts.

Sarcocysts. Compartmented, 260–1050 x 70–260 (mean 655 x 137) μm, with 2-layered wall 7–10 μm thick, outer layer 6–8 μm thick, with fine villar projections uniformly distant, inner layer glistening, 1–1.5 μm thick, continuing as septa within sarcocyst. Bradyzoites about 10–12 x 3–4 μm, each with several PAS-positive granules.

Remarks. This was probably the species that Crum, Fayer and Prestwood (1981) found in *O. virginianus* in West Virginia and transmitted to the cat but not the dog, opossum or raccoon. Its sporocysts were ellipsoidal, 11–13 x 7 (mean 11 x 8 [*sic*]) μm, without Stieda body, with residuum. Its prepatent period in the cat was 13 days and its patent period 24 days.

Sarcocystis spp.

The following discussion should be read in conjunction with the previous ones.

A *Sarcocystis* has been found in *O. virginianus* by Eisenstein and Innes, 1956; Blažek, Kotrly and Ippen, 1976; Karstad and Trainer, 1969; Prestwood, Pursglove and Hayes, 1976; Pond and Speer, 1979;

Mahrt and Colwell, 1980; and Crum and Prestwood, 1982. The relationship of this (these) form(s) to *S. odocoileocanis* and *S. odoi* needs to be determined.

Crum and Prestwood (1982) found 3 sizes of sporocyst representing at least 2 species of *Sarcocystis:* (1) 7 dogs shed sporocysts 13–17 x 9–12 (mean 15 x 11) μm 9–12 days after eating infected venison; these were probably *S. odocoileocanis;* (2) 1 cat shed sporocysts 11–13 x 7–9 (mean 12 x 9) μm 10 days after eating infected venison; this was probably *S. odoi;* (3) 1 red fox *Vulpes vulpes* shed sporocysts 11–16 x 9–11 (mean 14 x 10) μm 10 days after eating infected venison. They apparently thought that the cat and fox forms were the same species. The predominant species in the southeastern U.S. is the deer-dog form.

Host Genus *Alces*

***Eimeria alces* Arnastauskene, 1974** (Fig. 304)

Type Host. Moose *Alces alces.*

Oocyst Structure. Ovoid, 33–42 x 22–29 (mostly 34–39 x 23–27) μm, with rough, brownish, 2-layered wall, with micropyle 6–7 μm in diameter, without residuum or polar granule. Sporocysts elongate ovoid, 17–20 x 9-10 μm, with Stieda body and a few residual granules. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with clear globule at large end.

***Sarcocystis alceslatrans* Dubey, 1980**

Type Definitive Host. Coyote *Canis latrans.*

Other Definitive Host. Domestic dog *Canis familiaris.*

Type Intermediate Host. Moose *Alces alces.*

Location. Sarcocysts in tongue (not skeletal muscles) of moose; oocysts and sporocysts in small intestine mucosa of coyote and dog.

Oocyst Structure. Oocysts not described. Sporocysts ovoid, 14–17 x 8.5–10.5 (mean 14.5 x 8.8) μm in the coyote (Dubey, 1980) or 14–16 x 11–11.5 (mean 16 x 11) μm in the dog (Colwell and Mahrt, 1983), without Stieda body, with membrane-bound residuum. Sporozoites 8–10 x 2 μm.

Merogony. Pre-muscle meronts, if any, unknown. Sarcocysts compartmented, microscopic, thin-walled (about 1 μm thick), smooth, 223–829 x 143–255 (mean 328 x 188) μm, containing hundreds of

banana-shaped bradyzoites 3–3.5 μm wide; no metrocytes seen (Dubey, 1980).

Prepatent Period. 11 days in coyote (Dubey, 1980); 10–14 days in dog (Colwell and Mahrt, 1983).

***Sarcocystis* spp.**

Dubey (1980) found thick-walled (3.5-10.5 μm), microscopic, septate sarcocysts with a striated wall in the skeletal muscles of 1 of 11 moose *Alces alces* in Montana. The sarcocysts were 70–85 x 50–80 μm. They contained many banana-shaped bradyzoites 3–3.5 μm wide, but he saw no metrocytes.

Colwell and Mahrt (1981) found 2 kinds of sarcocyst in the esophagus, tongue and diaphragm of moose in Alberta, Canada. Type A was fusiform, compartmented, 1–7 x 0.5–0.7 mm, with tightly packed bradyzoites, with a wall 15 nm thick bearing numerous extensions 7–13 nm high folded against it, without fibrils in the ground substance, which was 42–55 nm thick, and with bradyzoites 10–13 μm long which had 22 subpellicular microtubules, loosely packed micronemes 53 nm in diameter, and 8–16 rhoptries. Type B sarcocysts were ovoid to spherical, compartmented, 0.5–2.0 mm long, each compartment containing loosely packed metrocytes, merozoites and debris, with a wall 12 nm thick bearing branched and folded projections 12 nm long, with ground substance 34–131 nm thick containing 20 nm fibrils, and with bradyzoites 9–12 μm long which had 22 subpellicular microtubules, tightly packed micronemes 60 nm in diameter, and 4–7 rhoptries.

Others who have reported sarcocysts of *Sarcocystis* spp. in the skeletal muscles of moose are Brooks (1903), deVos and Allin (1949), Kelly, Penner and Pickard (1958), Ippen et al. (1974), and Mahrt and Colwell (1980).

Fayer, Dubey and Leek (1982) fed 3 calves sporocysts (from the coyote) of *Sarcocystis* sp. originally from moose. The calves remained healthy, but one had intramuscular sarcocysts, suggesting to them either low infectivity for cattle by these forms or spurious natural infection.

***Toxoplasma heydorni* (Tadros and Laarman, 1976) Levine, 1977**

See under *Bos taurus*.

Host Genus *Rangifer*

***Eimeria arctica* Yakimoff, Matschoulsky and Spartansky, 1939**
(Fig. 40, Levine and Ivens, 1970)

Type Host. Reindeer *Rangifer tarandus*

Oocyst Structure. Ovoid, 32–38 x 26–30 (mean 35.5 x 28) μm, with yellowish, double-contoured wall 1.0–1.2 μm thick, with micropyle at small end, without residuum or polar granule. Sporocysts ovoid, 12–14 x 7–9 μm, without Stieda body, with residuum. Sporozoites comma-shaped.

***Eimeria mayeri* Yakimoff, Sokoloff and Matschoulsky, 1936**
(Fig. 42, Levine and Ivens, 1970)

Synonym. Eimeria sp. Yakimoff and Sokoloff, 1935.

Type Host. Reindeer *Rangifer tarandus.*

Oocyst Structure. Subspherical, seldom spherical, 16–20 x 14-16 (mean 17 x 15) μm, with double-contoured wall said in the text to have an indentation at one end but not so illustrated, without micropyle or residuum, with polar granule. Sporocysts elongate ovoid, pointed at both ends, 8-13 x 5.4 μm, without Stieda body or residuum. Sporozoites lying lengthwise in sporocysts, with a clear globule at one end.

***Eimeria muehlensi* Yakimoff, Sokoloff and Matschoulsky, 1936**
(Fig. 43, Levine and Ivens, 1980)

Type Host. Reindeer *Rangifer tarandus.*

Oocyst Structure. Ovoid, with one end tapered, 32–40 x 26–28 (mean 36 x 27) μm (only 7 oocysts seen), with 2-layered (described as tricontoured) wall 2 μm in total thickness, outer layer light yellowish, disappearing at the micropylar end, inner layer darker, almost brown, covering micropyle, with micropyle at tapered end, without residuum or polar granule. Sporocysts ovoid, 16–20 x 8-10 μm, with prominent Stieda body and residuum. Sporozoites comma-shaped, 12–14 x 4–6 μm, with clear globule at large end.

***Eimeria (?) polaris* Yakimoff and Sokoloff, 1935 emend. Levine and Ivens, 1970**
(Fig. 64, Levine and Ivens, 1970)

Synonym. Eimeria polaris Yakimoff and Sokoloff, 1935.

Type Host. Reindeer *Rangifer tarandus.*

Oocyst Structure. Ovoid, ellipsoidal, cylindroid or tapering to both ends with one end flattened, 24–35 x 15–21 μm, with yellowish, double-contoured wall, with micropyle in many but not seen in all, with polar granule. No sporulated oocysts seen.

***Eimeria tarandina* Yakimoff, Sokoloff and Matschoulsky, 1936**
(Fig. 44, Levine and Ivens, 1970)

Type Host. Reindeer *Rangifer tarandus.*

Oocyst Structure. Subspherical, sometimes spherical, 18–24 x 16–22 (mean 20 x 18) μm, yellowish or transparent, with double-contoured wall, without micropyle, residuum or polar granule. Sporocysts elongate ovoid, 12–14 x 6–8 μm, with broad, blunt, prominent Stieda body and residuum. Sporozoites with a clear globule at one end.

***Isospora rangiferis* Yakimoff, Matschoulsky and Spartansky, 1937**
(Fig. 272, Levine and Ivens, 1970)

Synonym. Isospora sp. Yakimoff, Sokoloff and Matschoulsky, 1936.

Type Host. Reindeer *Rangifer tarandus.*

Oocyst Structure. Ovoid or subspherical, 26–32 x 24–30 (mean 29 x 24.5) μm, with double-contoured wall, without micropyle or residuum, with polar granule. Sporocysts ovoid, described in text as 16–19 x 8–12 μm, listed in table as 12–16 x 8–12 μm, with double-contoured wall, prominent Stieda body and residuum. Sporozoites comma-shaped, with a clear globule at large end.

***Sarcocystis grueneri* Yakimoff and Sokoloff, 1934**

Type Definitive Host. Blue fox *Alopex lagopus.*

Other Definitive Hosts. Silver fox *Vulpes vulpes,* dog *Canis familiaris,* raccoon dog *Nyctereutes procyonoides* (Gjerde and Bratberg, 1984; Gjerde, 1984).

Type Intermediate Host. Reindeer *Rangifer tarandus.*

Location. Heart muscle.

Merogony. The sarcocysts are microscopic. According to Grüner (1927), they make the heart look as though it had been dusted with a fine powder. Hadwen (1922) said that the sarcocysts averaged 433 x 168 μm and the bradyzoites 16 x 7 μm. Yakimoff and Sokoloff (1934) said that the bradyzoites are 12–17 x 4.5–6 (mean 15 x 5) μm. Gjerde (1984) said that the sarcocysts are septate, micro- to macroscopic,

240–1,160 x 45–325 (mean 581 x 137) μm, with a thin wall without protrusions. Their bradyzoites are banana-shaped, 14–16.5 x 2–5 (mean 15 x 4) μm.

Sporogony. The sporocysts are 12–16 x 9–11 (mean 14 x 10) μm (Gjerde, 1984).

Remarks. Yakimoff and Sokoloff (1934) named this species from both the reindeer and maral "*Cervus canadensis asiaticus*," but it is extremely dubious that the same species would occur in both hosts. We are limiting the name to the form in the reindeer.

***Sarcocystis hardangeri* Gjerde, 1984**

Type Definitive Host. Unknown.

Type Intermediate Host. Reindeer *Rangifer tarandus.*

Location. Skeletal muscles of reindeer.

Merogony. Sarcocysts macroscopic, septate, ovoid to cylindrical, 900–2,845 x 450–1,575 (mean 1,675 x 625) μm, surrounded by a layer of fibrillar material 8–12 μm thick containing relatively few, irregularly spaced, tongue-shaped protrusions 20–35 x 3–5 x 2 μm with pointed, distal ends. Bradyzoites 11.5–15 x 3–5 (mean 13 x 4) μm.

Remarks. See under *S. tarandivulpes.*

***Sarcocystis rangi* Gjerde, 1984**

Type Definitive Host. Unknown.

Type Intermediate Host. Reindeer *Rangifer tarandus.*

Location. Skeletal muscles of reindeer.

Merogony. Sarcocysts long, slender, septate, 5,460–12,700 x 95–280 (mean 8,994 x 180) μm, with numerous very fine, flexible wall protrusions 8–10 x less than 0.5 μm. Bradyzoites banana-shaped, 12–16.5 x 2–5 (mean 14 x3) μm.

Remarks. See under *S. tarandivulpes.*.

***Sarcocystis rangiferi* Gjerde, 1984**

Type Definitive Host. Unknown.

Type Intermediate Host. Reindeer *Rangifer tarandus.*

Location. Skeletal muscles.

Merogony. Sarcocysts macroscopic, septate, 836–4,750 x 135–610 (mean 3,106 x 403) μm, with many tightly packed, somewhat tapering protrusions 11–16 x 4–8 (mean 13 x 7) μm forming a thick "wall,"

with a layer of fibrillar material containing nucleus-like structures investing the protrusions. Bradyzoites 10–13 x 3–4 (mean 12 x 4) μm.

Remarks. See under *S. tarandivulpes.*

***Sarcocystis tarandi* Gjerde, 1984**

Type Definitive Host. Unknown.

Type Intermediate Host. Reindeer *Rangifer tarandus.*

Location. Skeletal and heart muscles of reindeer.

Merogony. Sarcocysts micro- or macroscopic, slender, elongate, spindle-shaped, septate, 308–2,206 x 40–255 (mean 999 x 75) μm, with a wall bearing tightly packed protrusions 7–11 x 2–3 (mean 9 x 2) μm and not surrounded by a fibrillar layer. Bradyzoites banana-shaped, 10–13 x 2.5–4 (mean 11.5 x 3) μm.

Remarks. See under *S. tarandivulpes.*

***Sarcocystis tarandivulpes* Gjerde, 1984**

Synonym. Sarcocystis sp. Gjerde, 1984.

Type Definitive Host. Blue fox *Alopex lagopus.*

Other Definitive Hosts. Raccoon dog *Nyctereutes procyonoides.* Based on this and his previous work, Gjerde (1984) said that the silver fox *Vulpes vulpes* and dog *Canis familiaris* are also definitive hosts.

Location Skeletal muscles of reindeer; intestine of definitive hosts.

Merogony. Sarcocysts septate, slender, 610–2,000 x 45–130 (mean 970 x 76) μm, with short, knob-like wall protrusions about 1 μm long and wide.

Sporogony. Sporocysts 12–16 x 9–11 (mean 14 x 10) μm.

Remarks. It is unknown whether some of these names are synonyms of others. Cross-infection experiments should be carried out, between reindeer, other deer and other artiodacyls. In addition, sarcocysts of different ages should be compared.

***Sarcocystis* spp.**

Type Intermediate Host. Reindeer *Rangifer tarandus.*

Location. Esophagus, tongue and other muscles of reindeer.

Merogony. This form has macroscopic sarcocysts. Bergman (1913) said that they are the same size and shape as most of those of cattle. Hadwen (1922) said that they look much like those of *S. "tenella"* (i.e., *S. gigantea)* of sheep, with sarcocysts up to 2.25 mm long and averag-

ing 868 x 137 μm. He said that they tended to curl and often had a corkscrew appearance; their bradyzoites were 10 x 4 μm. Ippen et al. (1974) found sarcocysts that they did not describe in 11 of 32 reindeer.

***Besnoitia tarandi* (Hadwen, 1922) Levine, 1961**

Synonym. Fibrocystis tarandi Hadwen, 1922.

Type Definitive Host. Unknown.

Type Intermediate Host. Reindeer and caribou (both *Rangifer tarandus*).

Location. Fibrous connective tissues of *R. tarandus*, especially in periosteum and on surface of tendons.

Merogony. Meronts spherical, not compartmented, 100–450 (mean 275) μm in diameter, with 3-layered wall, outer layer thick and fibrous, with concentrically arranged fibers, middle layer clear and hyaline, inner layer forms a thin lining. Bradyzoites spindle-shaped, 7 x 2 μm in fixed material, with central nucleus.

Pathogenicity. Meronts cause pitting of bones and tendons; the resultant condition is known as "cornmeal disease."

Host Genus *Capreolus*

***Eimeria capreoli* Galli-Valerio, 1927** (Fig. 335)
(Figs. 53, 263, Levine and Ivens, 1970)

Type Host. Roe deer *Capreolus capreolus*.

Oocyst Structure. Oocysts ovoid or piriform, with the narrow end flattened, 25–36 x 19–26 (mean 30 x 21) μm, with smooth, yellowish, quite thick, 2-layered wall, outer layer pale, inner layer a heavy line, with micropyle at small end, without residuum or polar granule. Sporocysts elongate ovoid, 13–19 x 6–10 μm, with Stieda body, with some residual granules which disappear in several weeks. Sporozoites elongate, with one end broad and the other narrow, lying lengthwise head to tail in sporocysts, with clear globule at broad end.

Prepatent Period. Ten days, the largest number of oocysts being passed 12–13 days after inoculation (Pellérdy, 1955).

Cross-Transmission Studies. Mantovani, Borrelli and Ricci-Bitti (1970a) could not infect a calf, a lamb or a kid with this species. Pellérdy (1955) could not infect a 3-month-old roe deer with sheep or goat coccidia by placing it in the same stall with these animals for 2

months. Svanbaev (1979) failed to transmit this species from the roe deer to 22 lambs and 11 young saigas.

***Eimeria catubrina* Mantovani, Borrelli and Ricci-Bitti, 1970**
(Fig. 336)

Type Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Subspherical or ellipsoidal, 23–35 x 20–31 (mean 31 x 25) μm, with smooth, colorless, l-layered wall 0.8–l.4 μm thick, without micropyle, with residuum and polar granule. Sporocysts ovoid, 13–19 x 7–10 (mean 15 x 9) μm, with prominent Stieda body and residuum composed of small granules. Sporozoites elongate, with one end broad and the other narrow, lying lengthwise head to tail in sporocysts, with clear globule at the large end and possibly another at the narrow end.

Prepatent Period. 3 days.

Patent Period. About 3 months, although the number of oocysts is very small after about 10 days.

Cross-Transmission Studies. Mantovani, Borrelli and Ricci-Bitti (1970) could not infect a calf, a lamb or a kid with this species.

***Eimeria panda* Supperer and Kutzer, 1961** (Fig. 334)
(Figs. 47, 56, 57, Levine and Ivens, 1970)

Type Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Ovoid, sometimes bean-shaped, flattened at the small end, 25–35 x 14–20 μm, with a smooth, colorless, l-layered wall, with a micropyle at the small end, without residuum or polar granule. Sporocysts elongate ovoid or coffee-bean shaped, 10–13 x 5–8 μm, with or without Stieda body, with residuum. Sporozoites elongate, lying lengthwise in sporocysts, with clear globule at each end.

Cross-Transmission Studies. Mantovani, Borrelli and Ricci-Bitti (1970a) were unable to infect a calf, a lamb, or a kid with this species.

***Eimeria patavina* Mantovani, Borrelli and Ricci-Bitti, 1970**
(Fig. 333)

Type Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Bean-shaped or ellipsoidal, with one end slightly narrower than the other, 19–27 x 14-18 (mean 24 x 16) μm, with smooth, colorless, 1-layered wall 1–2 μm thick, with micropyle at narrow end, without residuum or polar granule. Sporocysts lemon-

shaped, 8–13 x 4–7 (mean 11.5 x 6) μm, said to be without Stieda body but illustrated with one, with residuum composed of small granules mainly between the sporozoites. Sporozoites elongate, with one end broad and the other narrow, lying lengthwise head to tail in sporocysts, with a clear globule at broad end.

Cross-Transmission Studies. Mantovani, Borelli and Ricci-Bitti (1970a) could not infect a calf, a lamb or a kid with this species.

***Eimeria ponderosa* Wetzel, 1942** (Fig. 331)
(Figs. 45, 46, 48, 55, Levine and Ivens, 1970)

Type Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Ovoid, with a drawn out and slightly flattened small end, 34–49 x 25–33 μm, with a 2(or 3?)-layered, yellowish-brown wall 2.5 μm thick (except somewhat thinner at the small end), outer layer rough, brownish, easily detached from inner one, inner layer transparent, scarcely 1 μm thick, with micropyle in outer layer but not inner one, without residuum or polar granule. Sporocysts ovoid, lemon-shaped, 19–22 x 9–10 μm, with Stieda body and residuum. Sporozoites elongate, 16 x 6 μm, with one end wider than the other, lying lengthwise head to tail in sporocysts, with clear globule near the broad end. Wetzel (1942) found relatively few oocysts at the surface after flotation in saturated NaCl solution, but greater numbers were present in the sediment. He therefore gave this species the name *ponderosa.*

Pellérdy (1955) and Boch and Lucke (1961) said that oocysts with a thick rough wall predominated at first, but that after sporulation (and perhaps due to the flotation solution) the outer layer came off so that the oocysts appeared smooth and thin-walled.

Patent Period. 15 days (Pellérdy, 1955).

Pathogenicity. Pellérdy (1955) found severe hemorrhagic inflammation of the small and large intestines of a roe deer that had died in the Budapest zoo, and thought that the coccidia had caused the condition; he found about 1,000 oocysts per microscope field in the large intestine.

Cross-Transmission Studies. Svanbaev (1979) failed to transmit this species from the roe deer to 22 lambs or 11 young saigas.

***Eimeria rotunda* Pellérdy, 1955** (Fig. 332)
(Figs. 51, 54, Levine and Ivens, 1970)

Type Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Generally spherical, sometimes subspherical to ovoid, 10–20 x 9–16 μm, with thin, smooth, colorless, 1-layered wall, without micropyle, residuum or polar granule. Sporocysts ovoid or spherical, 6–9 x 3–4 μm, with Stieda body and residuum. Sporozoites elongate, with one end broad and the other narrow, lying lengthwise head to tail in sporocysts, with a clear globule at the broad end.

Prepatent Period. 4 days (Pellérdy, 1955).

Cross-Transmission Studies. Mantovani, Borrelli and Ricci-Bitti (1970a) could not infect a calf, a lamb or a kid. Svanbaev (1979) failed to transmit this species from the roe deer to 29 lambs or 11 young saigas, although he did infect 40 roe deer.

According to Pellérdy (1955), this species was reported mistakenly as *E. zuernii* by Salhoff (1939), Ryšavý (1954) and others.

***Eimeria superba* Pellérdy, 1955** (Fig. 337)
(Fig. 49, Levine and Ivens, 1970)

Synonym. Eimeria auburnensis Christensen and Porter, 1939 of Böhm and Supperer, 1956.

Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Ovoid, sometimes asymmetrical or distorted, 43–55 x 28–34 μm, with 2-layered wall 3–4 μm thick, outer layer dark brown, rough, easily lost in potassium bichromate solution, inner layer smooth, clear, 1–1.3 μm thick, with micropyle, without residuum or polar granule. Sporocysts elongate ovoid, 16–26 x 10–12 μm, with Stieda body and residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with one end broad and the other narrow, with clear globule at broad end.

Prepatent Period. 18 days (Pellérdy, 1955).

Cross-Transmission Studies. Mantovani, Borrelli and Ricci-Bitti (1970a) could not infect a calf, a lamb or a kid with this species.

***Eimeria* sp. Boch and Lucke, 1961**
711g. 50, Levine and Ivens, 1970)

Type Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Ellipsoidal, 30–40 x 22–25 μm, with smooth, clear wall illustrated as composed of 1 layer, with indistinct micropyle, without residuum or polar granule. No other information given.

***Isospora capreoli* Svanbaev, 1958**

Type Host. Roe deer *Capreolus capreolus.*

Oocyst Structure. Ovoid or piriform, 40–46 x 28–32 (mean 43 x

31) μm, apparently with smooth, 2-layered, yellowish brown or brown wall 2–4 μm thick, inner layer radially striated, with prominent micropyle 4–5 μm in diameter, occasionally with inconspicuous micropylar cap, with residuum, without polar granule. Sporocysts piriform or ovoid, 19–25 x 11–16 (mean 22 x 13.5) μm. Sporozoites piriform or comma-shaped, 8–13 x 3–4 (mean 11 x 4) μm.

***Wenyonella markovi* Grobov and Ven'-Shun', 1963**
(Fig. 268, Levine and Ivens, 1970)

Type Host. Siberian roe deer *Capreolus capreolus pygargus.*

Oocyst Structure. Shaped like round-bottomed urn, bright yellow or yellow gray, 31–46 x 21–31 (mean 39 x 25) μm, with smooth, 2-layered wall 1.5–2.3 (mean 1.7) μm thick, outer layer thin, with fine stippling on its surface, inner layer thick, rough, with prominent micropyle 4–6 (mean 5) μm in diameter at small end, without residuum or polar granule. Sporocysts ellipsoidal, 9–12 x 8–12 (mean 11 x 10) μm, without Stieda body, substiedal body or residuum. Sporozoites 5–6 x 5 (mean 5.2 x 4.7) μm, each with a "polar granule."

***Sarcocystis capreoli* Levchenko, 1963**

Type Definitive Host. Unknown.

Type Intermediate Host. Roe deer *Capreolu capreolus.*

Location. Sarcocysts in striated muscles of roe deer.

Merogony. The sarcocysts are 190–810 x 30–75 μm and the bradyzoites in them are crescent-shaped, 8–14 x 2.5–5 μm.

Remarks. See the discussions of *S. capreolicanis* and *Sarcocystis* spp. for further information.

***Sarcocystis capreolicanis* Erber, Boch and Barth,** 1978

Type Definitive Host. Dog *Canis familiaris* and/or fox *Vulpes vulpes.*

Type Intermediate Host. Roe deer *Capreolus capreolus.*

Location. Sporocysts in feces of definitive host(s). Sarcocysts in striated muscles.

Oocyst Structure. Uncertain.

Merogony. Erber, Boch and Barth (1978) did not give the dimensions of the sarcocysts, but said that their wall had moveable hair-like protrusions 6–8 μm long and much less than 0.5 μm in diameter. The sarcocysts were compartmented. We saw no metrocytes in their

drawing. There is no merogony in the definitive host (Becker, Mehlhorn and Heydorn, 1979).

Cultivation. Becker, Mehlhorn and Heydorn (1979) cultivated this species, starting with bradyzoites from the roe deer, and obtained gamonts, oocysts and sporocysts in dog kidney but not in human fibroblast, cat lung or pig kidney cell cultures.

Remarks. The name *Sarcocystis capreolicanis* is either (1) a synonym of *S. capreoli* Levchenko, 1963, (2) a synonym of *S. sibirica* Machul'skii, 1947, or (3) a valid third species. We have not seen the Machul'skii paper; it is apparently not available in the United States. Erber, Boch and Barth (1978) did not mention either this or Levchenko's paper when they named *S. capreolicanis*. See also under *Sarcocystis* spp. below.

***Sarcocystis gracilis* Ratz, 1908**

Type Definitive Host. Unknown.

Type Intermediate Host. Roe deer *Capreolus capreolus.*

Location. Sarcocysts in deer striated muscles.

Merogony. Bradyzoites in sarcocysts 11–16 x 5–8 μm.

Remarks. This species was described by Istvan Ratz (not Stefan von Ratz, which is the German translation of his name) (1908, 1909, 1910) from Hungary, by Blažek, Kotrly and Ippen (1976) from Czechoslovakia, and by Krylov and Sapizhnikov (1965) from the USSR.

Babudieri (1932) said that the host of this species was the red deer *Cervus elaphus* (p. 482 of his text) or *Elaphus cervus* (his Table I). Levchenko (1963) said that Ratz had found it in *Cervus gracilis;* according to Ellerman and Morrison-Scott (1951), *C. gracilis* is a synonym of *C. nippon kopschi,* which occurs in China; *C. nippon,* they said, is the Sika deer, which does not occur in Hungary. Kalyakin and Zasukhin (1975) and Levine and Tadros (1980) also gave the host as *Cervus elaphus.* All were in error.

***Sarcocystis sibirica* Machul'skii, 1947**

Type Definitive Host. Unknown.

Type Intermediate Host. Roe deer *Capreolus capreolus.*

Location. Sarcocysts in roe deer striated muscles.

Merogony. Levchenko (1963) said that the sarcocysts are 0.1–1.6 x 0.08–0.15 mm and the bradyzoites 10–15 x 6–7 μm.

Remarks. We have not seen this paper; it is apparently not avail-

able in the United States. See the discussions of *S. capreolicanis* and *Sarcocystis* spp. for further information.

***Sarcocystis* spp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Roe deer *Capreolus capreolus.*

Location. Sarcocysts in roe deer striated muscles.

Remarks. The status of the *Sarcocystis* species of *C. capreolus* is in limbo. Kutzer and Hinaidy (1969) found what they called *Sarcocystis gracilis* (von Ratz, 1909) in 1% of 200 *C. capreolus* in Austria. Kavai and Sugar (1976) found *Sarcocystis* spp. in 88% of 99 *C. capreolus* in Hungary. Ippen et al. (1974) found them in 7 of 10 *C. capreolus* in Czechoslovakia and 12 of 37 in East Germany. Drost (1977) found them in the muscles of 96% of 500 adult and 58% of 100 young roe deer in East Germany. Blažek, Schramlová and Ippen (1978), Blažek, Schramlová, Ippen and Kotrlý (1978) and Schramlová and Blažek (1978) found a thin-walled (0.2–0.3 μm thick) *Sarcocystis* sp. and a thick-walled (0.45–0.75 μm thick) one with radial striations in 76% of 197 *C. capreolus* in Czechoslovakia. The primary sarcocyst wall of the thin-walled type formed long, fibril-less, finger-shaped protrusions distant from each other and running parallel to the sarcocyst surface. Between the protrusions were numerous bubble-like invaginations. The thick-walled type had massive, palisade-like protrusions lying close to each other. It had many fibrillar and tubular structures in the protrusions, and the primary wall occasionally formed shallow invaginations at the base of some protrusions. The unit membrane on the surface of some protrusions was slightly undulated and was covered with a layer of short, thick bars. They found that the dog (but not the cat) was the definitive host of the thin-walled species; it had a prepatent period of 10 days and its sporocysts were sporulated when passed in the feces, measured 15 x 10 μm and had a residuum. However, they said that they did not know whether this species was *S. capreoli* or *S. sibirica.* The infected muscle was pathological in almost 14% of the positive cases.

In East Germany, Drost and Graubmann (1974) found macroscopic sarcocysts in the muscles of 68% of 56 roe deer. With the trichinoscope they found sarcocysts in 96.5% of 200. They were 103–2,520 x 43–441 μm and compartmented.

In West Germany, Entzeroth, Scholtyseck and Greuel (1978) fed esophagus, diaphragm and peritoneal muscles of roe deer containing sarcocysts to a fox, a dog and a cat. They obtained (l) sporulated sporocysts 18.5 x 8.5 μm in the fox after a prepatent period of 8 days, and (2) sporulated sporocysts 15.6 x 10.0 μm in the dog after a prepatent period of 10–14 days; they had a patent period of 51 days. The cat did not pass any sporulated sporocysts. They concluded that roe deer muscles contain 3 structurally different sarcocysts.

In West Germany also, Erber, Boch and Barth (1978) found *Sarcocystis* spp. in 76% of 186 *C. capreolus* muscles by staining muscle smears, and 93% of 421 by a trypsin digestion technic. They found Type 1 (see below) in 94% of 72, Type 2 in 18% and Type 3 in 18%.

They fed tissues from the roe deer to 1 tiger, 16 house cats, 2 wildcats, 1 brown bear, 5 raccoons, 2 marsh lynxes, 2 red lynxes, 4 buzzards, 1 wood owl and 2 rooks (they gave no scientific names for these animals). Only dogs and foxes passed sporocysts. The prepatent period in the 2 foxes was 10–12 days and that in 10 dogs was 12–14 days. The sporocysts in both were 12–18 x 9–11 (mean 15 x 10) μm. They thought that this marked variation meant that the fox and dog are both hosts for 2 species of roe deer *Sarcocystis*.

They found the following sarcocysts:

Type 1. Sarcocyst wall about 1 μm thick, with essentially spherical protrusions about 0.8 μm in diameter. They called this type *Sarcocystis gracilis* v. Ratz, 1909. This form resembles the smooth sarcocyst of Entzeroth, Scholtyseck and Greuel (1978). Erber, Boch and Barth believed that both the dog and the fox are its definitive hosts.

Type 2. Sarcocyst wall with moveable, hair-like protrusions 6–8 μm long and much less than 0.5 μm in diameter. They called this form *Sarcocystis capreolicanis* n. sp. They thought that both the dog and fox were its definitive hosts. See Remarks under *S. capreolicanis* above for a discussion of the validity of this species name.

Type 3. Sarcocyst wall with rigid, finger-like protrusions 5–6 μm long and about 0.5 μm in diameter. They called this form *Sarcocystis* sp. and said that its definitive host was none of the animals that they tested.

They were unable to transmit Type 1 to a calf, a kid or a lamb.

They inoculated 4 roe deer with sporocysts from the dog. They found no sarcocysts in 2 of them. They found both Type 1 and Type

2 sarcocysts in 1 of them. The fourth aborted 2.5 months later. They found neither abortion bacteria nor sarcocysts in it. They found sarcocysts in it a year after inoculation.

Entzeroth (1980) found 6 types of sarcocyst in the muscles of naturally infected roe deer in West Germany. He infected the dog and red fox with at least some of them, obtaining sporocysts in feces in 8 days in the fox and in 13–14 days in the dog. He was unable to infect the raccoon, ferret, cat or martin *Martes foina.* He also failed to infect *Mus musculus* or a lamb with sporocysts from the dog. The sporocysts in the fox were 14 x 9 μm and those in the dog were 16 x 10 μm. They had a smooth, fairly thick wall, were ellipsoidal with one side rather flat, and contained a residuum but no Stieda body. Oocysts were 20–21 x 16–17 μm, with a very thin wall. They were in the lamina propria of the small intestine, and were most common in the duodenum and jejunum. There were no meronts in the dog. The patent period was 53 days in 1 dog.

He found tachyzoites in the spleen, liver and lymph nodes of the roe deer 33 days after feeding sporocysts from the dog. He found meronts 38–43 μm in diameter on day 45 in satellite cells, endothelial cells, myoblasts, connective tissue cells or leukocytes in the tongue, esophagus and diaphragm. They contained tachyzoites 4–5 x 2–3 μm, with a typical apical complex; more than 30 were in a section. The sarcocysts had both metrocytes and merozoites. Experimental infections of roe deer fawns with high sporocyst doses led to death. The definitive hosts had no pathologic manifestations.

He was aware of earlier work and nomenclature of roe deer *Sarcocystis,* but obviously felt that he was dealing with more than one species and was unable to differentiate them (except on the basis of fine structure of the sarcocyst wall, which was not helpful in this case).

***Toxoplasma* spp.**

Entzeroth, Scholtyseck and Greuel (1978) fed esophagus, diaphragm and peritoneal muscles of *C. capreolus* to a cat and found unsporulated oocysts 12 x 11 μm in its feces 8 days later. After sporulating these oocysts and feeding them to mice, they found typical *Toxoplasma gondii* "cysts" in their brains and typical *Toxoplasma* (syn., *Hammondia) hammondi* "cysts" in their muscles. After a prepatent period of 11 days, they also found unsporulated oocysts 13.1 x 11.6 μm

resembling those of "the small form of *Isospora bigemina (Hammondia)* described by Heydorn (1973) and Rommel and Seyerl (1976) in the feces of the fox." These oocysts did not infect mice.

Host Family GIRAFFIDAE

Host Genus *Giraffa*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Giraffe *Giraffa camelopardalis.*

Location. Sarcocysts in striated muscles of giraffe.

Merogony. Kaliner, Grootenhuis and Protz (1974) found microscopic sarcocysts only.

Host Family ANTILOCAPRIDAE

Host Genus Antilocapra

***Eimeria antilocaprae* Huizinga, 1942 emend. Levine and Ivens, 1970**

(Fig. 52, Levine and Ivens, 1970)

Synonym. Eimeria antelocaprae Huizinga, 1942.

Type Host. Pronghorn *Antilocapra americana.*

Oocyst Structure. Ellipsoidal, broadly ellipsoidal or subspherical, 25–35 x 21–30 (mean 31 x 26) μm, with faint dull yellow-green, 2-layered wall 2.0–2.2 μm thick, outer layer smooth, light yellow-green or blue, about ⅔ the total thickness, inner layer brown, without micropyle, with residuum in 86% of freshly sporulated oocysts but disintegrating into irregularly shaped granules indistinguishable from polar granules 2–4 weeks after sporulation (Todd, Hammond and O'Gara, 1967), with polar granule. Sporocysts about 16.5 x 9 μm or 13–17 x 8–11 (mean 15 x 9) μm, with Stieda body and residuum. Sporozoites with one end broad and the other narrow, lying lengthwise head to tail in sporocysts, with clear globule at each end and nucleus between them.

***Eimeria* sp.**

Type Host. Pronghorn *Antilocapra americana.*

Oocyst Structure. Ovoid, 34–35 x 17–20 μm, with rough, 2-layered wall about 2.5 μm thick, with micropyle 3–4 μm in diameter surrounded by collar-like thickening of the outer oocyst wall, with residuum, without polar granule. Sporocysts 12-14 x 5–7 μm, with Stieda body and residuum.

Remarks. Todd, Hammond and O'Gara (1967) found only 3 oocysts of this form and were uncertain whether it was actually a new species.

***Sarcocystis* sp.**

Dubey (1980) found thin-walled (about 1 μm), smooth, microscopic, compartmented sarcocysts in 1 of 22 *A. americana* in Montana. They were 127–297 x 63–95 (mean 169 x 76) μm and contained many bradyzoites 3–3.5 μm wide. He saw no metrocytes. He fed a dog infected muscle from a pronghorn, but found no oocysts or sporocysts in its feces or intestine thereafter.

Host Family BOVIDAE

Host Genus *Tragelaphus*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Bushbuck *Tragelaphus scriptus.*

Location. Sarcocysts in *T. scriptus* striated muscles.

Merogony. Mandour and Keymer (1970) found 2 sizes of microcyst: (l) about 130–250 x up to 65 μm, and (2) 11–13 x up to 3 μm. The bradyzoites in these sarcocysts were 11–13 x 2–3 μm in sections, 10 x 3 μm in thin smears and 13 x 5 μm in thick smears.

***Sarcocystis* sp. Ippen et al., 1974**

Type Definitive Host. Unknown.

Type Intermediate Host. Sitatunga *Tragelaphus spekei.*

Location. Sarcocysts in *T. spekei* striated muscles.

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Greater kudu *Tragelaphus strepsiceros.*

Location. Sarcocysts in striated muscles of kudu.

Merogony. Mandour and Keymer (1970) found microscopic sarcocysts only. They were about 150 or more by up to 105 μm and contained bradyzoites 10–15 x 3–5 μm.

***Besnoitia besnoiti* (Marotel, 1913) Henry, 1913**

Type Definitive Host. Cat *Felis catus.*

Type Intermediate Host. Ox *Bos taurus.*

Other Intermediate Hosts. Kudu *Tragelaphus strepsiceros,* etc.

Location. Endothelium of cardiovascular system and conjunctival sclera of kudu.

Remarks. Basson (1965), McCully et al. (1966) and Bigalke et al. (1967) found this species in *T. strepsiceros* in the Kruger National Park, South Africa. There were whitish meronts a little less than 0.5 mm in diameter attached to the endothelium and intima of the blood vessels. They were most numerous in the peripheral veins, especially of the limbs and jugular veins, but were also frequently seen on the valves and were also found in the lymph channels and subcutis of some animals. A few were present in the conjunctival sclera of some animals. No clinical manifestations were seen.

See the discussions under *Bos* and *Connochaetes* below for further information on this species.

Host Genus *Taurotragus*

***Eimeria canna* Triffitt, 1924**

(Fig. 58, Levine and Ivens, 1970)

Type Host. Eland (canna antelope) *Taurotragus oryx* (syn., *Orias canna).*

Oocyst Structure. Ovoid, 23–24 x 16–20 μm, with 3-layered wall, outermost layer very delicate, middle layer greenish, hyaline, about 1 μm thick except at ends where it is about 0.5 μm thick, inner layer a delicate membrane about 0.5 μm from middle layer, with slightly flattened micropyle, rarely with residuum or polar granule. Sporocysts ovoid, 12–17 x 5–7 μm, with Stieda body, and residuum. Sporozoites

elongate, club-shaped, lying lengthwise head to tail in sporocysts, with a clear globule at the large end and sometimes another one near the small end.

Cross-Transmission Studies. Triffitt (1924) could not transmit this species, which she found in the London zoo, to the domestic rabbit.

***Eimeria triffittae* Yakimoff, 1934 emend. Levine and Ivens, 1970** (Fig. 61, Levine and Ivens, 1970)

Synonym. Eimeria triffitt Yakimoff, 1934.

Type Host. Eland (canna antelope) *Taurotragus oryx* (syn., *Orias canna).*

Oocyst Structure. Ellipsoidal, 21–24 x 15-19 (mean 21 x 18) μm, with wall illustrated as l-layered, with inner line heavier than outer, without micropyle, residuum or polar granule. Sporocysts elongate with rounded ends, 9 x 4–6 μm; sporocyst residuum described as not "clearly visible" and illustrated as absent. Sporozoites piriform, with one end rounded and the other pointed.

***Eimeria* sp. Van Wettere, 1966**

Type Host. Eland *Taurotragus oryx.*

Oocyst Structure. Ellipsoidal, 14–22 x 11–17 (mean 17 x 14) μm, with colorless, thin wall, without micropyle or residuum; polar granule not mentioned. Sporocysts not described.

Pathogenicity. Van Wettere (1966) said that this organism caused a very fluid dysentery in an eland calf in Rwanda.

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Eland *Taurotragus oryx.*

Location. Sarcocysts in eland striated muscles.

Merogony. Kaliner, Grootenhuis and Protz (1974) found microscopic sarcocysts (microcysts) only.

Host Genus *Boselaphus*

***Eimeria nilgai* Pande, Bhatia, Chauhan and Garg, 1970** (Fig. 302)

Type Host. Nilgai *Boselaphus tragocamelus.*

Location. Unknown; oocysts found in feces.

Oocyst Structure. Subspherical, 17–24 x 15–20 (mean 21 x 17.5)

μm, with smooth, 2-layered wall 1.3 μm thick, outer layer yellowish green, inner layer brown, without micropyle, residuum or polar granule. Sporocysts broadly ovoid, 8–14 x 3–6 (mean 10 x 5) μm, with Stieda body and residuum. Sporozoites 10.5 x 3 μm, with one end broadly rounded and the other tapering, lying lengthwise head to tail in sporocysts, with central nucleus and a large, clear globule at the broad end.

***Eimeria tragocamelis* Bhatia, 1968** (Fig. 338)

Type Host. Nilgai *Boselaphus tragocamelus.*

Oocyst Structure. Ovoid to ellipsoidal, 20–29 x 16–20 (mean 24 x 19) μm, with 2-layered wall 1.3–1.5 μm thick, thinner at the narrow end, outer layer greenish yellow, 1 μm thick, inner layer thinner, light brown, perhaps with micropyle, without residuum or polar granule. Sporocysts ovoid, 10–13 x 5–7 (mean 12 x 6) μm, with Stieda body as a flat, dark cap, with residuum in form of sparse granules. Sporozoites elongate and tapering, lying lengthwise head to tail in sporocysts, with 3 or 4 clear globules.

***Eimeria yakimovi* Rastegaieff, 1929** (Fig. 321)
(Fig. 67, Levine and Ivens, 1970)

Type Host. Nilgai *Boselaphus tragocamelus.*

Oocyst Structure. Ovoid, 27–41 x 20–29 μm, with a smooth, 2-layered wall 1–1.5 μm thick, outer layer yellowish-green, inner layer dark yellowish-brown, with micropyle, without residuum or polar granule. Sporocysts ellipsoidal or ovoid, 13–17 x 6–8 μm, with or without Stieda body, with or without residuum. Sporozoites 11–15 x 4–6 μm, vermicular or slightly piriform, lying lengthwise head to tail in sporocysts, with a clear globule at the large end.

Host genus *Tetracerus*

***Eimeria chausinghi* Pande, Bhatia, Chauhan and Garg, 1970**
(Figs. 306, 307)

Type Host. Four-horned antelope *Tetracerus quadricornis.*

Oocyst Structure. Ovoid, 20–27 x 15–21 (mean 25 x 18) μm, with smooth, 2-layered wall 1.3 μm thick, outer layer light yellowish, inner layer dark yellowish green, without micropyle, residuum or polar granule. Sporocysts ellipsoidal, with somewhat narrowed ends, 13–

16 x 5.6 [*sic*] (mean 14 x 6.6) μm, with Stieda body and residuum. Sporozoites 11–14 x 3–4 (mean 13 x 4) μm, with one end broadly rounded and the other pointed, lying lengthwise head to tail in sporocysts, with large clear globule and central nucleus.

Host Genus *Bubalus*

***Eimeria alabamensis* Christensen, 1941**
(Figs. 182, 278, Levine and Ivens, 1970)
See the discussion below under *Bos*.

***Eimeria ankarensis* Sayin, 1969**
(Figs. 282, 283, Levine and Ivens, 1970)

Host. Water buffalo *Bubalus bubalis*.

Prevalence. Fairly common.

Oocyst Structure. Elongate ovoid, 32–43 x 25–29 (mean 39 x 26) μm, with yellowish brown, 2-layered wall 3.0–3.5 μm thick, lined by a membrane, outer layer thick, rough, inner layer very thick, dark brown, with micropyle, without residuum or polar granule. Sporocysts elongate, almost ellipsoidal, 18–23 x 8–10 (mean 21 x 9) μm, with Stieda body and residuum. Sporozoites elongate, rather comma-shaped, lying lengthwise head to tail in sporocysts, with 2 clear globules each.

Cross-Transmission Studies. Sayin (1969) was unable to transmit this species to the ox by feeding 3-week-old calves 50 sporulated oocysts each.

***Eimeria auburnensis* Christensen and Porter, 1939**
(Fig. 284, Levine and Ivens, 1970)
See the discussion below under *Bos*.

***Eimeria azerbaidschanica* Yakimoff, 1933**

Synonym. Eimeria azerbaidjhanaica Yakimoff, 1933 *(lapsus calami)*.

Type Host. Water buffalo *Bubalus bubalis*.

Oocyst Structure. Cylindrical, but with one side somewhat concave and the other somewhat convex, 45 x 22 μm, without micropyle. No other structural information given.

Remarks. Pellérdy (1974) considered this a *nomen dubium*. We agree.

***Eimeria bareillyi* Gill, Chhabra and Lall, 1963**
(Figs. 65, 66, 202, Levine and Ivens, 1970)

Synonym. Eimeria bubalis Abdussalam and Rauf, 1956 of Yasin and Abdussalam, 1958.

Type Host. Water buffalo *Bubalus bubalis.*

Location. Epithelial cells of villi of jejunum (Pande, Bhatia and Chauhan, 1971).

Oocyst Structure. Piriform, with a bluntly truncate small end, 24–35 x 15–25 μm, with a smooth, homogeneous, yellowish to darkish brown, 2-layered wall about 1 μm thick except at the micropylar end, where it is thin, lined by a membrane, with micropyle, with or without residuum, without polar granule. Sporocysts lemon-shaped or ovoid, 15–18 x 6–9 μm, with Stieda body and residuum. Sporozoites banana-shaped, about 10 x 4 μm, lying lengthwise head to tail in sporocysts, with a clear globule at the large end and sometimes 1 or 2 smaller ones, with central nucleus.

Merogony. Apparently in epithelial cells of the jejunal villi.

Gamogony. Apparently in epithelial cells of the jejunal villi. Microgamonts 20–37 x 18–25 (mean 27 x 21) μm, with many slightly curved, rod-like microgametes 3 μm long and some small masses of residual bodies. Macrogametes 23–35 x 14–17 (mean 24 x 15) μm. Oocysts inside affected epithelial cells 23–27 x 13–17 (mean 25 x 15) μm.

Pathogenicity. Gill, Chhabra and Lall (1963) observed heavy discharges of oocysts without clinical signs. They found as many as 1.9 million oocysts per gram of feces in water buffalo calves and fewer in adults.

***Eimeria bovis* (Zublin, 1908) Fiebiger, 1912**
(Fig. 276, Levine and Ivens, 1970)

See the discussion below under *Bos.*

***Eimeria brasiliensis* Torres and Ramos, 1939**
(Fig. 285, Levine and Ivens, 1970)

See the discussion below under *Bos.*

***Eimeria bukidnonensis* Tubangui, 1931**
(Fig. 191, Levine and Ivens, 1970)

See the discussion below under *Bos.*

***Eimeria canadensis* Bruce, 1921**
(Fig. 275, Levine and Ivens, 1970)
See the discussion below under *Bos*.

***Eimeria cylindrica* Wilson, 1931**
(Fig. 281, Levine and Ivens, 1970)
See the discussion below under *Bos*.

***Eimeria ellipsoidalis* Becker and Frye, 1929**
(Fig. 277, Levine and Ivens, 1970)
See the discussion below under *Bos*.

***Eimeria gokaki* Rao and Bhatavdekar, 1959**
(Fig. 70, Levine and Ivens, 1970)

Synonym. Eimeria brasiliensis Torres and Ramos, 1939 of Patnaik (1965); [*non*] *Eimeria brasiliensis* Torres and Ramos, 1939.

Type Host. Water buffalo *Bubalus bubalis*.

Oocyst Structure. Ovoid, 22–31 x 18–25 μm, with thin, homogenous, slightly yellowish brown wall, with micropyle and micropylar cap. Sporocysts 16 x 7 μm, with residuum.

***Eimeria ovoidalis* Ray and Mandal, 1961**
(Fig. 69, Levine and Ivens, 1970)

Synonym. Eimeria wyomingensis Huizinga and Winger, 1942 of Patnaik (1965); [*non*] *Eimeria wyomingensis* Huizinga and Winger, 1942.

Type Host. Water buffalo *Bubalus bubalis*.

Oocyst Structure. Ovoid, 32–40 x 20–28 (mean 35.5 x 24) μm, with pinkish orange wall, with micropyle, without micropylar cap or residuum. Sporocysts ovoid, 14–16 x 8–9 μm, with Stieda body and residuum. Sporozoites 8–9 x 4–5 μm.

Cross-Transmission Studies. Ray and Mandal (1961) transmitted this species experimentally to zebu calves. The oocysts in the zebu calves were 20–39 x 16–24 μm, but when these were given to water buffalo calves, oocysts of the original size were discharged.

***Eimeria subspherica* Christensen, 1941**
(Figs. 188, 279, Levine and Ivens, 1970)
See the discussion below under *Bos*.

***Eimeria thianethi* Gwéléssiany, 1935**
(Fig. 68, Levine and Ivens, 1970)

Type Host. Water buffalo *Bubalus bubalis.*

Other Hosts. Ox *Bos taurus,* zebu *B. indicus.*

Oocyst Structure. Ovoid, grayish yellow, 34–49 x 26–34 (mean 43 x 29) μm, with 2-layered wall 2 μm thick, outer layer thin and homogeneous, inner layer thick, with transverse striations, with or without micropyle, apparently without residuum or polar granule. Sporocysts lemon-shaped, with pointed ends, 22 x 9.5 μm, with residuum.

***Eimeria wyomingensis* Huizinga and Winger, 1942**
(Fig. 274, Levine and Ivens, 1970)

See the discussion below under *Bos.*

***Eimeria zuernii* (Rivolta, 1878) Martin, 1909**
(Fig. 280, Levine and Ivens, 1970)

See the discussion below under *Bos.*

***Sarcocystis fusiformis* (Railliet, 1897) Bernard and Bauche, 1912**

Synonyms. Balbiania fusiformis Railliet, 1897; *Balbiania siamensis* von Linstow, 1903; *Balbiania* sp. de Jongh, 1885; *Sarcocystis siamensis* (von Linstow, 1903); *Sarcocystis bubali* Willey, Chalmers and Philip, 1904.

Type Definitive Host. Cat *Felis catus.*

Type Intermediate Host. Water buffalo *Bubalus bulalis.*

Remarks. Zaman, Robertson and Papadimitriou (1980) described the scanning electron microscopic appearance of the sarcocysts. There are 2 walls, the sarcocysts are compartmented, and the bradyzoites have a micropore.

For further information, see Levine and Ivens, 1981.

***Sarcocystis levinei* Dissanaike and Kan, 1978**

Type Definitive Host. Dog *Canis familiaris.*

Type Intermediate Host. Water buffalo *Bubalus bubalis.*

Oocyst Structure. Oocysts not described. Sporocysts ellipsoidal, 12.5–17 x 8–12 μm, without Stieda body, with residuum (Chauhan et al., 1977; Tongson and Calingasan, 1980).

Prepatent Period. 17–20 days in dog (Chauhan et al., 1977).

Patent Period. More than 148 days (Chauhan et al., 1977).
For further information, see Levine and Ivens, 1981.

Host Genus *Bos*

***Eimeria alabamensis* Christensen, 1941**
(Figs. 181, 183, 184, Levine and Ivens, 1970)

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* water buffalo *Bubalus bubalis.*

Location. Primarily small intestine, also cecum and upper colon in heavy infections.

Oocyst Structure. Ovoid, 13–26 x 11–18 μm, with smooth, very pale yellow, 2-layered wall about 0.6–1.3 μm thick, inner layer a thin membrane without micropyle, residuum or polar granule (except for some tiny scattered fragments which might or might not be polar granule fragments). Sporocysts ellipsoidal, with one end bullet-like, 8–18 x 4–6 μm, with tiny Stieda body, with or without residual granules. Sporozoites lie lengthwise head to tail in sporocysts, with 1–3 clear globules.

Merogony. The endogenous cycle takes place in the nucleus of the intestinal cells. At first the sporozoites are spindle-shaped. The young meronts lie in a parasitophorous vacuole in the apical cells of the tips of the villi. They grow to maturity in 3 days, being 7–12 x 6–10 μm at 3 days and 8–18 x 5–14 μm at 8 days. They contain 16–32 merozoites. There is probably more than 1 asexual generation (Davis, Bowman and Boughton, 1957).

See also below under Cultivation for descriptions of merogony in tissue culture.

Gamogony. Gamonts are formed in the nuclei of the epithelial cells of the villi. Two or 3 microgamonts and 3–5 macrogametes or oocysts per host cell nucleus are not uncommon. The microgamonts are 8–25 x 7–21 (mean 16 x 11.5) μm. The macrogametes are 7–20 x 7–12 (mean 12 x 9) μm (Davis, Bowman and Boughton, 1957).

Prepatent Period. 6–11 days.

Patent Period. One to 13 days.

Pathogenicity. E. alabamensis is essentially nonpathogenic under field conditions, although it may cause signs in the laboratory, and diarrhea, and even death if many millions of oocysts are given (Davis,

Bowman and Boughton, 1957; Davis, 1943; Soekardono, Ernst and Benz, 1975).

Immunity. Soekardono, Ernst and Benz (1975) said that calves initially inoculated with 10 million or 80 million oocysts and then reinoculated 3 weeks later with 100 million oocysts had greatly reduced oocyst discharges following reinoculation.

Cultivation. Sampson, Hammond and Ernst (1971) cultivated *E. alabamensis* in monolayer primary cell cultures of bovine embryonic intestine, kidney, spleen and thyroid, and in cell line cultures of bovine embryonic trachea and synovium as well as in established cell line cultures of Madin-Darby bovine kidney, human intestine and Syrian hamster kidney. They obtained 0.5–1.7% development to mature meronts. In all cultures except bovine embryonic synovium, human intestine and Syrian hamster kidney they got large meronts 11–19 x 8–11 (mean 14 x 10) μm with 6–14 short, stubby merozoites, each with 2 clear globules, at 2–3 days. In all cultures they got small meronts 5–13 x 5–9 (mean 10 x 6) μm containing 6–10 long, slender merozoites, each with 2 clear globules, at 3 days. The meronts were seldom intranuclear.

Sampson and Hammond (1972) found that the intracellular sporozoites had a conoid, 1–4 micropores, 22 subpellicular microtubules, micronemes and as many as 6 rhoptries.

***Eimeria auburnensis* Christensen and Porter, 1939**
(Figs. 141–175, Levine and Ivens, 1970)

Synonyms. Eimeria ildefonsoi Torres and Ramos, 1939; *E. khurodensis* Rao and Hiregaudar, 1954; *Eimeria* sp. Pop-Cenitch and Bordjochki, 1959.

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* water buffalo *Bubalus bulalis.* Ryff and Bergstrom (1975) said that they had found *E. auburnensis* in the American bison *Bison bison* in Wyoming.

Location. Middle and lower third of small intestine.

Oocyst Structure. Ovoid, somewhat flattened at small end, 32–46 x 19–30 μm with smooth, heavily mammillated or rarely rough, 2-layered wall 1.0–1.8 μm thick, possibly lined by a thin membrane, outer layer colorless to yellowish orange, pink-orange or lavender, inner layer greenish or orange-green, with micropyle and polar gran-

ule, without residuum. Sporocysts elongate ovoid, almost ellipsoidal, 15–23 x 6–11 μm, with wall about 0.2 μm thick, with Stieda body and residuum. Sporozoites elongate, rather comma-shaped, 15–21 x 3–5 μm, lying lengthwise head to tail in sporocysts, with a large clear globule at the large end and sometimes 1–2 small ones elsewhere.

Merogony. Giant meronts occur throughout the small intestine but mostly 6–12 m anterior to the ileocecal valve. They are 78–250 x 48–150 (mean 140 x 92) μm and are usually located in the cells of the reticular connective tissue deep in the lamina propria near the muscularis mucosae. (In contrast, the giant meronts of *E. bovis* occur in the endothelial cells lining the lacteals of the villi). They mature 10 days after inoculation, being 134–338 x 95–172 (mean 178 x 114) μm at that time, contain thousands of merozoites, and occupy the whole width of the crypt. The mature merozoites within the meronts are about 11 μm long.

The second-generation meronts occur in the subepithelium in cells of mesodermal origin in the distal part of the villi 2–8 m anterior to the ileocecal valve. They are mature at 12–15 days, at which time they are 6–12 x 5–9 (mean 8.5 x 6) μm and contain 4–11 (mean 7) merozoites each. These are spindle-shaped and 7–9 x 1–2 (mean 8 x 1.5) μm (Chobotar, 1968; Chobotar and Hammond, 1967, 1969; Hammond, Clark and Miner, 1961; Davis and Bowman, 1962; Chobotar, Hammond and Miner, 1969).

Gamogony. The gamonts occur 12–19 DAI in the subepithelium in mesenchymal-mesodermal cells of the small intestine. The mature microgamonts are 36–288 x 27–150 μm and contain thousands of microgametes each. The microgametes are 4–8 x 0.5–0.75 μm and have 2–3 flagella 10–12 μm long. The macrogametes are about 18 μm in diameter at 18 days (Hammond, Clark and Miner, 1961; Davis and Bowman, 1962; Chobotar, 1968; Chobotar and Hammond, 1969; Hammond, Scholtyseck and Chobotar, 1969; Scholtyseck, Mehlhorn and Hammond, 1972).

Prepatent Period. 16–24 days.

Patent Period. 2–8 days.

Pathogenicity. This species is moderately pathogenic and may cause profuse, watery green diarrhea accompanied by slight apathy, straining and even dysentery. The signs appear about 9 days after inoculation (i.e., about 15 days before the first oocysts appear in the feces) and continue for about 5 days.

Cross-Transmission Studies. Sayin (1969) said that he infected 3-week-old calves *(Bos taurus)* with *E. auburnensis* from the water buffalo.

Cultivation. Clark and Hammond (1969) cultivated this species from the sporozoite to the mature first-generation meront stage in Madin-Darby bovine kidney, embryonic bovine trachea and embryonic bovine spleen tissue cultures, but not in human intestinal cell (Intestine 407) tissue cultures. The first mature meronts were seen 9 days after inoculation.

Remarks. See Pellérdy (1974) for information on the synonymy of this species.

***Eimeria bombayansis* Rao and Hiregaudar, 1954**

Type Host. Zebu *Bos indicus.*

Geographic Distribution. Asia (India).

Oocyst Structure. Ellipsoidal, sometimes with one side relatively flat and the other convex, 32–40 x 20–25 (mean 37 x 22) μm, with smooth, transparent, homogeneous, pale yellowish brown wall 1.0–1.5 μm thick, thicker around micropyle, with micropyle, without residuum. Sporocysts ovoid, 12–15 μm long, with residuum. Sporozoites 4–6 μm long, rounded.

Remarks. This name may be a synonym of either *E. auburnensis* or *E. canadensis.*

***Eimeria bovis* (Züblin, 1908) Fiebiger, 1912**

(Figs. 77–126, Levine and Ivens, 1970)

Synonyms. Coccidium bovis Züblin, 1908; *Eimeria canadensis* Bruce, 1921 (in part); *E. smithi* Yakimoff and Galouzo, 1927; *Eimeria (Globidium) bovis* (Züblin, 1908) Reichenow, 1953; *E. aareyi* Rao and Bhatavdekar, 1959; (?) *Globidium fusiformis* Hassan, 1935.

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* probably carabao or water buffalo *Bubalus bubalis,* wisent or European bison *Bison bonasus,* banteng *Bibos banteng,* and perhaps American bison *Bison bison.*

Location. First-generation meronts in the endothelial cells of the lacteals in the villi of the posterior half of the small intestine. Second-generation meronts in the epithelial cells of the cecum and colon. Gamonts generally in the epithelial cells of the glands of the cecum and colon, but may extend up into the terminal 1–1.3 m of the small intestine in heavy infections.

Oocyst Structure. Ovoid to ellipsoidal, 23–34 x 17–23 (mean about 27–29 x 20–21) μm (oocysts in water buffalo 23–43 x 15–26 μm), with smooth (rarely roughened), 2-layered wall, outer layer colorless, about 1.3 μm thick, inner layer brownish yellow, about 0.4 μm thick, with inconspicuous micropyle, without residuum or polar granule. Sporocysts elongate ovoid, 10–18 x 5–9 μm, with inconspicuous Stieda body and residuum. Sporozoites elongate, 14–17 x 3–4 μm, one end smaller than the other, lying lengthwise head to tail in sporocysts, usually with a clear globule at each end.

Merogony. There are 2 asexual and 1 sexual endogenous generations in the life cycle. The first asexual generation occurs in the endothelial cells of the lacteals in the villi of the posterior half of the small intestine. These cells become detached from the lacteal lining and lie free and greatly swollen in the lumen of the lacteals. The meronts are first found 5 days after inoculation. They grow to giant size, becoming mature 14–18 days after inoculation, when they are 207–435 x 134–267 (mean 303 x 281) μm and contain 55,000-170,000 (mean 120,000) merozoites. They are easily visible to the naked eye as whitish balls; their presence was first pointed out by Boughton (1942) as a macroscopic lesion that could be used in diagnosing coccidiosis.

Second-generation meronts occur in the epithelial cells of the cecum and colon. Mature meronts average 10 x 9 μm in tissue sections and contain 30–36 merozoites averaging 3.5 x 1.2 μm. Living second-generation merozoites are 6–7 (mean 6.2) μm long (Hammond, Andersen and Miner, 1963).

Gamogony. The sexual stages generally occur only in the cecum and colon, but in heavy infections they may be found in the terminal 1–1.3 m of the small intestine. They are in the epithelial cells of the intestinal glands. They first appear 17 days after inoculation (Scholtyseck, Mehlhorn and Hammond, 1971; Scholtyseck and Hammond, 1970; Hammond and Scholtyseck, 1970).

Prepatent Period. 15–20 days.

Patent Period. 1–3 weeks.

Pathogenicity. E. bovis is one of the 2 most pathogenic bovine coccidia. It may cause diarrhea and/or dysentery, tenesmus, temperatures as high as 106.6 F (41.4 C), and even death.

The most severe pathologic changes occur in the cecum, colon and

terminal 0.3 m of the ileum. They are due to the gamonts. At first the mucosa is congested, edematous and thickened, with petechiae or diffuse hemorrhages. Its lumen may contain a large amount of blood. Later the mucosa is destroyed and sloughed, and a patchy or continuous membrane forms over its surface. The submucosa may also be destroyed. If the animal survives, both mucosa and submucosa are later replaced.

Immunity. Infection of calves with *E. bovis* produces partial immunity against subsequent exposure (Senger et al., 1959).

Cross-Transmission Studies. Wilson (1931) was unable to infect pigs or goats with *E. bovis* from the ox. Becker (1933) could not infect the Norway rat. Sayin (1969) said that he infected 3-week-old calves *(Bos taurus)* with *E. bovis* from the water buffalo.

Cultivation. E. bovis has been cultivated from sporozoites to first-generation merozoites in embryonic bovine trachea cell cultures, and to second-generation merozoites and even oocysts in Madin-Darby bovine kidney and embryonic bovine trachea cell cultures (Hammond, Fayer and Miner, 1969; Dubremetz and Elsner, 1979). Speer and Hammond (1973) found that second-generation meronts developed in monolayers of Madin-Darby bovine kidney and primary embryonic bovine kidney cells and kidney-cell aggregates 48–108 hours after they had been inoculated with first-generation merozoites. They contained 24–36 merozoites 4.5 x 1.4 μm. Microgamonts and macrogametes were mature at 96–120 hours, being 15 μm in diameter and 19.5 x 15 μm, respectively. They saw zygotes at various stages of oocyst wall formation and oocysts 24 x 15 μm at 120–168 hours. A crescent body was present in the parasitophorous vacuole of some meronts and gamonts.

***Eimeria brasiliensis* Torres and Ramos, 1939** (Fig. 342)
(Figs. 178–189, 269, 270, Levine and Ivens, 1970)

Synonyms. Eimeria boehmi Supperer, 1952; *Eimeria orlovi* Basanova, 1952; *Eimeria helenae* Donçiu, 1961.

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* water buffalo *Bubalus bubalis,* and possibly American bison *Bison bison.*

Oocyst Structure. Ellipsoidal, sometimes slightly ovoid, 31–49 x 21–33 μm (31–44 x 20–29 μm in the water buffalo), with micropyle

and moundshaped or flat cap, with generally smooth, brownish yellow, 2-layered wall, outer layer 1–2 μm thick at the sides and 1 μm thick at the end opposite the micropyle, inner layer a brownish membrane. Oocyst surface occasionally covered by round, partially coalescent yellowish plaques about 5 μm in diameter, which form an incomplete additional layer on the surface, giving it a rough appearance; some of these plaques may be partially scaled off of the oocysts. Oocyst generally without residuum but tiny scattered granules present in some oocysts and some amorphous material in others, with or without polar granule. Sporocysts elongate ellipsoidal, 16–22 x 7–10 μm, with small, dark Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with a clear globule at each end.

***Eimeria bukidnonensis* Tubangui, 1931**

(Figs. 185, 190, 193, Levine and Ivens, 1970)

Type Host. Zebu *Bos indicus.*

Other Hosts. Ox *Bos taurus,* banteng *Bibos banteng* and presumably water buffalo *Bubalus bubalis.*

Oocyst Structure. Piriform, 34–54 x 26–41 μm, with micropyle, without micropylar cap, with yellowish brown, punctate, radially striated, 2-layered wall about 3–4 μm thick, inner layer a rather thick membrane which may be slightly wrinkled at the small end, without residuum or polar granule. Sporocysts elongate, somewhat pointed at both ends, about 12–21 x 9–12 μm, without residuum or with a few tiny, scattered granules, with or without Stieda body. Sporozoites with one end wider than the other, lying lengthwise head to tail in sporocysts, with a clear globule at each end.

Prepatent Period. 9–25 days.

Patent Period. About 7–12 days.

Pathogenicity. Apparently not pathogenic.

***Eimeria canadensis* Bruce, 1921**

(Figs. 129–131, Levine and Ivens, 1970)

Synonym. Eimeria zurnabadensis Yakimoff, 1931.

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* banteng *Bibos banteng,* wisent or European bison *Bison bonasus,* water buffalo *Bubalus bubalis* and presumably American bison *Bison bison.*

Oocyst Structure. Slightly ovoid or ellipsoidal, 28–39 x 20–29 (mean 33–34 x 23–24) μm, usually with smooth wall but sometimes with a roughened one, with 2-layered wall, outer layer colorless to yellowish, about 0.5 μm thick, inner layer clear, yellow, 1.3 μm thick, lined by a thin membrane, with inconspicuous micropyle, generally without residuum or with single polar granule; a number of splintered or a small amount of amorphous material polar granules may be present at the micropylar end of some oocysts. Oocysts in the water buffalo 25–37 x 18–28 μm. Sporocysts elongate ovoid, 13–22 x 6–10 μm with small Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 2–3 clear globules each.

Cultivation. This species has been cultivated from the sporozoite to the first-generation merozoite in various bovine cell cultures (Mueller, DeVos and Hammond, 1973, Mueller, 1978, 1980; Mueller and Speer, 1981).

***Eimeria cylindrica* Wilson, 1931**

(Figs. 138–140, Levine and Ivens, 1970)

Synonym. [*non*] *Eimeria cylindrica* Ray and Das Gupta, 1936 (syn. of *E. gupti* Bhatia, 1938).

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* water buffalo *Bubalus bubalis.*

Oocyst Structure. Elongate ellipsoidal, with relatively straight sides, 16–34 x 12–19 (mean 21–27 x 13–15) μm, with colorless, smooth, 1–2-layered wall about 1.2 μm thick at the sides and bottom and about 0.7 μm thick at one end, apparently without micropyle, without residuum, with polar granule shattered into many small fragments. Sporocysts elongate ellipsoidal, 9–16 x 4–6 (mean 15 x 5) μm, with thin to somewhat thick wall, with or without Stieda body, usually with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 1 or more rather indistinct clear globules and a central vesicle which may be a nucleus.

Prepatent Period. Ten days.

Patent Period. Ten days.

Pathogenicity. Probably nonpathogenic in the ox (See Willi and Eckert, 1972).

Cross-Transmission Studies. Wilson (1931) was unable to infect pigs or goats with this species.

***Eimeria ellipsoidalis* Becker and Frye, 1929**
(Figs. 132–137, Levine and Ivens, 1970)

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* water buffalo *Bubalus bubalis,* wisent or European bison *Bison bonasus,* banteng *Bibos banteng* and gayal *Bibos gaurus* (syn., *Bos frontalis).*

Location. Small intestine.

Oocyst Structure. Ellipsoidal to ovoid, 12–32 x 10–29 μm, with smooth, colorless, 1–2-layered wall sometimes lined by a membrane which is often wrinkled at the small end, without micropyle but with wall slightly thinner at one end than the other, without residuum, ordinarily without polar granule. Sporocysts elongate ovoid, with almost flat sides, 11–17 x 5–7 μm, with or without inconspicuous, small flat Stieda body, with residuum. Sporozoites elongate, larger at one end than the other, 11–14 x 2–3 μm, lying head to tail in sporocysts, with a clear globule at the large end and another near the middle, 24 subpellicular microtubules, a protrusible conoid composed of spirally-arranged fibrils, 2 rings anterior to the conoid, a polar ring at the anterior end of the microtubules and forming the anterior end of the inner membrane, rhoptries, micronemes, endoplasmic reticulum, Golgi apparatus, mitochondria with tubular cristae, micropores, lipoidlike bodies, oval polysaccharide bodies and ribosomes (Becker and Frye, 1929; Christensen, 1941, Levine and Ivens, 1967; Willi and Eckert, 1972; Sayin, 1970; Nyberg and Hammond, 1965; Bhatia et al., 1968; Roberts and Hammond, 1970).

Merogony. Mature meronts in epithelial cells of small intestine mucosa, 9–16 x 7.5–15 (mean 11 x 9) μm, with 24–36 merozoites 8–11 x 1–2 μm, usually lying parallel to each other (Boughton, 1945; Hammond, Sayin and Miner, 1962, 1963).

Gamogony. Gamonts and oocysts in posterior ½ or ⅔ of the small intestine. Mature gamonts present 10 days after inoculation in epithelial cells near the bottoms of the crypts. Mature microgamonts 12–16.5 x 11–16.5 (mean 15 x 13) μm. Microgametes 2–3 μm long (Hammond, Sayin and Miner, 1962, 1963).

Prepatent Period. 8–13 (mean 10) days.

Patent Period. 4–16 days.

Pathogenicity. This species often causes diarrhea in calves 1–3 months old, but is rarely if ever fatal.

Immunity. Previous infection produces some degree of immunity.

Cross-Transmission Studies. Sayin (1969) infected 3-week-old calves *(Bos taurus)* with *E. ellipsoidalis* from the water buffalo.

Cultivation. Speer and Hammond (1971) cultivated this species in Madin-Darby bovine kidney and embryonic bovine trachea cultures. Mature first-generation meronts appeared in 5–14 days; they were 11–20 x 10–17 (mean 16 x 13) μm and contained 18–42 (mean 30) merozoites 8–11 x 1–2 μm; most had a residuum.

***Eimeria illinoisensis* Levine and Ivens, 1967**

(Fig. 201, Levine and Ivens, 1970)

Type Host. Ox *Bos taurus.*

Oocyst Structures. Ellipsoidal or slightly ovoid, 24–30 x 19–23 (mean 26–27 x 21) μm, with smooth, colorless, 1–layered wall about 1.3 μm thick with a pale tan inner surface which looks like a membrane in intact oocysts, without definite micropyle, but one end of oocyst wall slightly thinner and flatter, with darker boundaries, than the other, without residuum or polar granule. Sporocysts elongate ovoid, with one end slightly tapered, 13–17 x 6–8 (mean 15–16 x 6.5–7) μm, with small, flat to knoblike (in isolated sporocyst) Stieda body, with residuum. Sporozoites elongate, with one end larger than the other, lying lengthwise head to tail in sporocysts, with 2 or more clear globules (Levine and Ivens, 1967; Sayin, 1970).

***Eimeria kosti* Elibihari and Hussein, 1974**

Type Host. "Cow."

Location. Abomasum.

Oocyst Structure. Spherical to subspherical, occasionally slightly elongate, 13–17 x 12–15 (mean 15 x 14) μm, with clear, refractile wall, with micropyle "distinct in 3 oocysts" but number of oocysts examined not stated. No other structural information given.

Gamogony. According to Elibihari and Hussein (1974), the oocysts, microgamonts and macrogametes are in epithelial cells of the base of the mucosal glands near the muscularis mucosae but sometimes in epithelial cells nearer the surface of the mucosa of the abomasum. These glands are partially or completely destroyed. The macrogametes are 15 x 13 μm. Two microgamonts 14–15 x 12–13 μm were seen. Other forms were in epithelial cells toward the middle of the mucosal glands and were 6–9 x 4–7 μm. Still other small to large forms were also seen.

Remarks. The above description is obviously inadequate, and this "species" is included here only for the sake of completeness. This organism should be studied further.

***Eimeria mundaragi* Hiregaudar, 1956**

Type Host. Zebu *Bos indicus.*

Oocyst Structure. Ovoid, 36–38 x 25–28 μm, with smooth, transparent, pale yellow or yellow wall 0.3 μm thick (slightly thicker at micropylar end), with distinct micropyle 0.5 μm in diameter, without residuum or polar granule. Sporocysts ovoid, 15 x 9 μm, thinning at the pointed end, with residuum. Sporozoites 4–6 x 1–3 μm, finely granular.

Remarks. This may or may not be a valid species (see Levine and Ivens, 1970).

***Eimeria pellita* Supperer, 1952**

(Figs. 194, 195, Levine and Ivens, 1970)

Type Host. Ox *Bos taurus.*

Oocyst Structure. Ovoid, with a flattened small end, 32–42 x 22–30 μm, with relatively thick, 2-layered, dark brown wall bearing numerous small, uniformly distributed protuberances on its surface which give the wall a velvety appearance, with micropyle at small end, without residuum, with or without polar granule. Sporocysts elongate ovoid, 14–20 x 6–9 μm, with or without a small Stieda body, with residuum. Sporozoites lie lengthwise head to tail in sporocysts, with 2 clear globules. (See also Ernst and Todd, 1977).

***Eimeria subspherica* Christensen, 1941**

(Figs. 186, 187, 189, Levine and Ivens, 1970)

Type Host. Ox *Bos taurus.*

Other Hosts. Zebu *Bos indicus,* water buffalo *Bubalus bubalis.*

Oocyst Structure. Spherical to subspherical, 9–14 x 8–13, μm with smooth, pale yellowish, 1–2-layered wall about 1 μm thick, without micropyle, residuum or polar granule. Sporocysts elongate ovoid, often with rather flat sides, 6–10 x 2–5 μm, with small Stieda body, without substiedal body, usually without residuum. Sporozoites wider at one end than the other, lying lengthwise head to tail in sporocysts, with a clear globule at the large end.

Prepatent Period. 7–18 days.

Patent Period. 4–15 days.

***Eimeria thianethi* Gwéléssiany, 1935**

See the discussion above under *Bubalus*.

***Eimeria wyomingensis* Huizinga and Winger, 1942**

(Figs. 198–200, Levine and Ivens, 1970)

Synonyms. ?Eimeria bukidnonensis Tubangui, 1931 of Christensen (1938a); [*non*] *E. bukidnonensis* Tubangui, 1931.

Type Host. Ox *Bos taurus*.

Other Hosts. Zebu *Bos indicus,* water buffalo *Bubalus bubalis*.

Oocyst Structure. Ovoid, 36–46 x 26–32 (mean 40 x 28) μm, with yellowish brown to brownish yellow, speckled and somewhat rough, 1–layered wall about 2–3.5 μm thick, lined by a membrane, with micropyle at small end, without residuum or polar granule. Sporocysts ellipsoidal, with somewhat narrow ends, about 18 x 9 μm, with tiny, flat Stieda body, generally without residuum. Sporozoites with one end wider than the other, about 7–8 x 5 μm at the broader end, lying lengthwise head to tail in sporocysts, with a large, clear globule.

Prepatent Period. 13–15 days.

Patent Period. 1–7 (mean 3.6) days.

Remarks. Ernst and Benz (1980) transmitted this species to calves by feeding sporulated oocysts or sporocysts.

***Eimeria zuernii* (Rivolta, 1878) Martin, 1909**

(Figs. 71–76, Levine and Ivens, 1970)

Synonyms. Cytospermium zurnii Rivolta, 1878; *Eimeria bovis* (Züblin, 1908) Fiebiger, 1912 in part; *Eimeria canadensis* Bruce, 1921 in part; *Eimeria zuerni* (Rivolta, 1878) Martin, 1909 of Pellérdy (1965).

Type Host. Ox *Bos taurus*.

Other Hosts. Zebu *Bos indicus,* water buffalo or carabao *Bubalus bubalis*.

Location. Meronts and merozoites in epithelial cells of small intestine, cecum and colon. Gamonts and gametes in epithelial cells of lower small intestine, cecum, colon and rectum, rarely in upper small intestine.

Oocyst Structure. Subspherical, subovoid, ovoid or sometimes ellipsoidal, 12–29 x 10–21 (mean 17–21 x 14–17) μm, with smooth, colorless, 1–2-layered wall about 1 μm thick (except a little thinner at the small end if there is one), without micropyle or residuum, without

or with 1 or more polar granules. Sporocysts elongate ovoid, 7–14 x 4–8 (mean 9–12 x 5–6) μm, with tiny Stieda body, with or without residuum. Sporozoites elongate, lying head to tail in sporocysts, with a clear globule at the large end. Free sporozoites 8–10 x 2–3 (mean 9 x 2) μm.

Merogony. First-generation meronts are in the lamina propria of the lower ileum. They are giant meronts 202–225 x 78–115 (mean 167 x 122) μm and contain thousands of merozoites when mature at 14–16 days. Second-generation meronts are in the epithelial cells of the cecum and proximal colon 16–20 days after inoculation. They are 13–22 x 13–21 μm and contain an average of 3 merozoites 13–17 x 1–3 (mean 16 x 2) μm (Stockdale, 1976, 1976a, 1977).

Gamogony. Macrogametes and microgamonts are in the epithelial cells of the cecum and proximal colon beginning 16 days after inoculation. The macrogametes are 18–24 x 16–24 (mean 21 x 17) μm, and the microgamonts 22–26 x 16–19 (mean 23 x 17) μm. Peak oocyst production occurs on days 19 and 20 (Stockdale, 1976, 1976a).

Prepatent Period. 15–17 days.

Patent Period. About 11 days.

Pathogenicity. E. zuernii is the most pathogenic coccidium of cattle. In acute infections it causes a bloody diarrhea of calves. At first the feces are streaked with blood. The diarrhea becomes more severe; bloody fluid, clots of blood, and liquid feces are passed; and straining and coughing may cause this mixture to spurt out as much as 2–3 m. The animal's rear quarters may look as though they had been smeared with red paint. Anemia, weakness and emaciation accompany the dysentery; secondary infections, especially pneumonia, are common. This acute phase may continue for 3 or 4 days. If the calf does not die in 7–10 days, it will probably recover.

E. zuernii may also be associated with a more chronic type of disease. Diarrhea is present, but there may be little or no dysentery. The animals are emaciated, dehydrated, weak and listless, with rough hair coats, drooping ears, and sunken eyes.

A generalized catarrhal enteritis involving both the small and large intestines is present. The lower small intestine, cecum and colon may be filled with semifluid, bloody material. Large or small areas of intestinal mucosa may be eroded and destroyed, and the mucous membrane may be thickened, with irregular whitish ridges in the large intestine or smooth, dull gray areas in the small intestine or cecum.

Diffuse hemorrhages are present in the intestines in acute cases and petechial hemorrhages in mild ones.

One of the most puzzling types of coccidiosis in cattle is winter coccidiosis, which is most commonly caused by *E. zuernii.* It occurs primarily in calves, and occurs during or following cold or stormy weather in the winter. Because this is the period when the temperature is too low for oocyst sporulation, other factors must be operative (Roderick, 1928). Marsh (1938) thought that coccidia must normally be present in the intestine without causing appreciable damage until the host's resistance is decreased by exposure to cold, change in feed, etc. Marquardt (1962) gave evidence that supported this idea; he found that little or no transmission occurred during the winter in Montana and thought (1976) that winter coccidiosis due to *E. zuernii* was caused by activation of arrested endogenous stages in the tissues of the host. Hammond, Sayin and Miner (1965) obtained similar results in Utah. However, the factors involved in winter coccidiosis still remain undetermined because the disease cannot be produced at will. Are the life cycles of all bovine coccidia self-limiting as they appear to be? Is the continual presence of oocysts in the feces due to repeated reinfections, or is it due to "hidden" merogony in some parenteral location? Further research is needed to elucidate the matter. For further discussion, see Hammond (1964) or Levine (1973).

Immunity. Niilo (1969) found that feeding Hereford calves 300,000 oocysts at 5 months of age protected them partially against subsequent challenge with 300,000 oocysts at 7 and 9 months of age. Repeated doses of 100 sporulated oocysts soon after birth did not stimulate immunity.

Cross-Transmission Studies. Sayin (1969) infected 3-week-old calves *(Bos taurus)* with *E. zuernii* from the water buffalo.

Cultivation. Speer, DeVos and Hammond (1973) cultivated *E. zuernii* from the sporozoite to the mature large meront in Madin-Darby bovine kidney, embryonic bovine trachea and embryonic bovine kidney cell cultures.

Remarks. According to Fitzgerald (1975), bovine coccidiosis is the fifth most important bovine disease in the U.S. It occurs most frequently east of the Mississippi River and in beef cattle. About 77 million young cattle are susceptible to coccidiosis each year, about 3.85 million are treated, and about 80,000 or more die of the disease. By far the most important species is *E. zuernii.*

***Isospora aksaica* Bazanova, 1952**

Type Host. Ox *Bos taurus.*

Oocyst Structure. Spherical, 26 μm in diameter, with smooth, 2-layered wall 1.6 μm thick with a light blue outer layer and a greenish, dingy rose inner one, presumably without micropyle, presumably without residuum, possibly with polar granules. Sporocysts ellipsoidal or spherical, 22 x 15 μm, presumably without residuum. Sporozoites spherical, bean-shaped or ellipsoidal, 15 x 11 μm.

Remarks. This is probably not a valid species. See Levine and Mohan (1960).

***Isospora bisonis* Mandal and Choudhury, 1983**

Type Host. Gaur *Bos gaurus.*

Location. Feces.

Oocyst Structure. Ovoid, 25–32 x 18–23 (mean 29 x 22) μm, with a 2-layered wall 1 μm thick, the outer layer smooth, the inner layer slightly thicker than the outer one, with a micropyle and micropylar cap, without a residuum or polar granule. Sporocysts spherical, 11–12 μm in diameter, with a wall 0.8 μm thick, without a Stieda body, with a residuum. Sporozoites bean-shaped, slightly curved, 5–6 x 1–2 (mean 5 x 2) μm, with a clear globule at the broad end, lying lengthwise head to head in the sporocysts.

Remarks. This may not be a valid separate species.

***Isospora felis* Wenyon, 1923**

Type Definitive Host. Domestic cat *Felis catus.*

Transport Hosts. All the following are experimental: house mouse *Mus musculus,* Norway rat *Rattus norvegicus,* golden hamster *Mesocricetus auratus,* domestic cat *Felis catus,* domestic dog *Canis familiaris,* ox *Bos taurus.*

Remarks. Fayer and Frenkel (1979) and Wolters, Heydorn and Laudahn (1980) found that the ox is a transport host. The latter said that the prepatent period in the cat after feeding ox muscle was 5–6 days for 1 isolate and up to 52 days for another. However, that of the second changed abruptly to 6 days after a few cat-to-cat oocyst passages.

For other information, see Levine and Ivens (1981).

***Isospora* sp. Levine and Mohan, 1960**

(Fig 267, Levine and Ivens, 1970)

Type Host. Ox *Bos taurus,* ox-zebu *Bos taurus-B. indicus* hybrids.

Other Hosts. Presumably zebu *Bos indicus* and water buffalo *Bubalus bubalis.*

Oocyst Structure. Usually subspherical, 21–33 x 20–32 (mean 27 x 25) μm, with smooth, colorless, pale lavender or pale yellowish, 1-layered wall about 1 μm thick, sometimes apparently lined by a thin membrane, without micropyle or residuum, with several irregular, refractile polar granules. Sporocysts lemon-shaped, 14–20 x 10–12 (mean 17 x 11) μm, quite thick-walled, with Stieda body, a button-shaped cap and a substiedal body, with finely granular residuum. Sporozoites sausage-shaped, not arranged in any particular order in sporocyst. Sporocyst residuum and sporozoites enclosed in a membrane, forming more or less of a ball within the sporocyst.

Remarks. This is probably *I. passeris* of the house sparrow.

***Cryptosporidium muris* Tyzzer, 1907**

Synonym. Cryptosporidium bovis Barker and Carbonell, 1974.

Host. Ox Bos taurus.

Other Host. Ox-zebu hybrid *Bos taurus-B. indicus* (Santa Gertrudis).

This species has been transmitted from calves to pigs, lambs, man, rats, mice, guinea pigs and chicks, and has caused diarrhea in most of them (e.g., Tzipori et al., 1980, 1982; Moon and Bemrick, 1981; Reese et al., 1981; Levine, 1984).

Location. Small intestine.

Oocyst Structure. Spherical, 2–4 μm in diameter, with 4 sporozoites and a large residuum. The oocysts may be attached to the epithelium by a specialized attachment zone (Pohlenz et al., 1978, 1978a; Barker and Carbonell, 1974).

Sporulation. Occurs while the oocysts are still attached to the intestinal cells (Pohlenz et al., 1978).

Merogony. There are 2 generations of meront. They are attached by a specialized attachment zone to the microvillar (brush) border of the epithelial cells of the ileum. The first-generation meronts contain 8 crescentic merozoites each, and the second-generation ones contain 4 merozoites each. Both meronts have a residuum; they are spherical, 3–4 μm in diameter (Barker and Carbonell, 1974; Pohlenz et al., 1978, 1978a; Pearson and Logan, 1978; Panciera, Thomassen and Garner, 1971).

Gamogony. This, like merogony, occurs in the brush border of the intestinal villar epithelial cells.

Pathogenicity. Infected calves have diarrhea; edema and mild reticuloendothelial cell hyperplasia of the mesenteric lymph nodes have been reported (Schmitz and Smith, 1975; Pohlenz et al., 1978).

Remarks. A number of human cases of cryptosporidial diarrhea have been reported in people who have had contact with infected calves (e.g., Reese et al., 1981, 1982; Anderson et al., 1982). There is no doubt that bovine cryptosporidiosis is a zoonosis.

***Sarcocystis cruzi* (Hasselmann, 1923) Wenyon, 1926**

Synonyms. Miescheria cruzi Hasselmann, 1923; *Sarcocystis fusiformis* Railliet, 1897 of Babudieri (1932) and *auctores* in part; *([non] S. fusiformis* Railliet, 1897); *Sarcocystis iturbei* Vogelsang, 1938; *S. marcovi* Vershinin, 1975 in part; *S. bovicanis* Heydorn, Gestrich, Mehlhorn and Rommel, 1975; *S. hirsuta* Moulé, 1888 of Vershinin (1974) and others; *Isospora rivolta* sporocysts of Gassner (1940) and *auctores* in part; *I. bigemina* large form of Mehlhorn, Heydorn and Gestrich (1975) and Heydorn, Mehlhorn and Gestrich (1975) in part; *Endorimospora hirsuta* (Moulé, 1888) Tadros and Laarman, 1976.

Type Definitive Host. Dog *Canis familiaris.*

Other Definitive Hosts. Coyote *Canis latrans,* wolf *C. lupus,* red fox *Vulpes vulpes,* raccoon *Procyon lotor.*

Type Intermediate Host. Ox *Bos taurus.*

Location. First-generation meronts in endothelial cells of arterioles of cecum, colon, kidney, pancreas and cerebrum of ox. Second-generation meronts in mesenteric lymph nodes, adrenals, cecum, cerebrum, cerebellum, diaphragm, esophagus, eye, heart, intestine, kidney, liver, lung, pancreas, spleen, muscles, testis, thyroid, tongue and urinary bladder of ox. Last-generation meronts (sarcocysts) in striated muscles (including myocardium) of ox. Sexual stages in lamina propria cells just beneath the epithelium of the center third of the villi of the small intestine of the dog.

Oocyst Structure. Sporocysts in dog feces asymmetrically ellipsoidal, 13–22 x 6–15 μm, with a colorless, 1-layered wall, without a Stieda body, with a residuum. In the coyote they are 13–21 x 9–18 μm. The sporulated oocysts in coyotes lack a micropyle, polar granule or residuum. The sporozoites lie lengthwise in the sporocysts, are elongate with one end broader than the other, are about 10 x 3 μm when alive or 9 x 2 μm in sections, and contain several PAS-positive granules (Dubey, 1982a).

Merogony. There are 3 generations of meront in the ox. Sporozoites have been found in the endothelial cells of mesenteric lymph node arteries 7 days after experimental inoculation (Dubey, 1981b). The first-generation meronts are in or beneath the endothelial cells of small and medium-sized arteries in the cecum, large intestine, kidney, pancreas and cerebrum. They can be found 15–16 days after oral inoculation with sporocysts. These meronts are 17–52 x 7–28 μm and contain 8–200 (mean 103) nuclei.

The merozoites are formed by endopolygeny. The meronts contain 100–350 merozoites 5–6 x 1 μm plus 2–4 relatively small residual bodies. The merozoites contain most of the organelles, including micropores, characteristically found in coccidian merozoites (Fayer, 1977; Dubey, Speer and Douglass, 1981; Dubey, Speer and Epling, 1982; Speer and Dubey, 1982).

The second-generation meronts have been found in the kidney glomeruli and also in the adrenal glands, cecum, cerebellum, cerebrum, diaphragm, esophagus, eye, auricle and ventricle of the heart, ileum, jejunum, kidney, liver, lung, mesenteric lymph nodes, pancreas, spleen, skeletal muscles, testis, thyroid, tongue and urinary bladder of calves on days 26–33. They are usually in endothelial cells of the blood vessels or near the vessels. They are 8–27 x 4–13 (mean 15 x 9) μm and contain 3–50 (mean 27) nuclei or tachyzoites 7–8 x 2–3 μm. Merogony takes place by endodyogeny. These tachyzoites go to the muscles and form sarcocysts (i.e., third-generation meronts).

Sarcocysts containing metrocytes and merozoites were found by Fayer and Johnson (1974) in the ventricle of a calf 33 days after inoculation. Sarcocysts containing only metrocytes can be found on day 34, and sarcocysts containing merozoites and metrocytes on days 40–54; there are no first- or second-generation meronts at this time. The sarcocysts develop in parasitophorous vacuoles in the host muscle cells. At first the vacuole has a single unit membrane, but it becomes thicker and forms a primary wall up to 20–25 nm thick. This primary wall becomes folded in alternating long and short club-shaped protrusions 0.13–0.6 μm long. The combined protrusions look like a very thin cyst wall under the light microscope. Later all the protrusions become about 3 μm in maximum length. They do not contain fibrils. Even old sarcocysts appear to be relatively thin-walled under the light microscope; the protrusion layer is not more than 1 μm thick because the protrusions are folded over.

As the sarcocyst grows, it becomes divided by thin septa (not visible with the light microscope) into numerous chambers filled with parasites. By 76 days, only bradyzoites are present. Both metrocytes and merozoites reproduce by endodyogeny. It takes about 3 months for the bradyzoites to become mature enough for ready transmission to dogs.

The metrocytes are 7 x 5 μm and the merozoites 11–14 μm long. There are many micronemes which fill the anterior third of the cell, and 14 rhoptries in a single longitudinal section. There are 22 subpellicular microtubules (Vershinin, 1974; Mehlhorn, Heydorn and Gestrich, 1975; Gestrich, Mehlhorn and Heydorn, 1975; Mehlhorn et al., 1975; Pacheco, Sheffield and Fayer, 1978).

Gamogony. This takes place in the lamina propria of the small intestine of the dog or other definitive host (Heydorn and Rommel, 1972; Fayer, 1974; Sheffield and Fayer, 1980). In the coyote the mature microgamonts are 6–9 x 4–7 μm and contain 3–11 slender microgametes 3.5–4 x less than 0.5 μm; the macrogametes are 7–8.5 x 7–8 μm (Dubey, 1982). The oocyst wall begins to form on day 7, and sporogony begins on day 8. When the sporulated sporocysts are first passed in the feces, some of them are in pairs, but later on all are single.

Prepatent Period. 8–33 days (Heydorn and Rommel, 1972; Fayer, Mahrt and Johnson, 1973; Fayer and Leek, 1973; Fayer, 1974, 1977).

Patent Period. Several weeks in the dog, 14–21 days in the fox and 8–22 days in the raccoon (Heydorn and Rommel, 1972; Fayer, Johnson and Hildebrandt, 1976; Fayer, 1977).

Pathogenicity. S. cruzi is not pathogenic in the dog or coyote, but may be extremely so in the ox. Fayer (1974) found neither gross nor microscopic lesions in the intestines of infected dogs.

Fayer and his associates have studied the experimental disease in cattle extensively. Both dogs and coyotes have been used as a source of infection. Calves fed 250,000–1 million sporocysts developed cachexia, anorexia and accelerated heart rates 23–35 days after inoculation, became unable to stand, and were killed or died 26–54 days after inoculation. They had generalized lymphadenopathy and hemorrhage of the serous membranes throughout the peritoneal cavity, and hemorrhage of the pericardium, myocardium and dorsal surface of the cerebellum. *S. cruzi* causes oligocythemic anemia, leukocytic shift to the left and elevation of serum SGOT, LDH and CPK levels

during the acute phase of the disease. The total serum and plasma proteins decrease during the acute phase and then increase, becoming higher than those of control calves at 7–8 weeks. The initial decrease is due to serum albumin decrease, whereas the later increase is due to IgM and IgG immunoglobulin increase. The calves have thymic atrophy with accompanying T cell decrease, lymphoid follicular exhaustion and loss with accompanying B cell decrease, and decreased responses to phytohemagglutinin and pokeweed mitogen (Fayer, 1974; Fayer, Mahrt and Johnson, 1973; Fayer and Johnson, 1973, 1975; Mahrt and Fayer, 1975; Fayer and Lunde, 1977; Fayer and Lynch, 1979; Frelier, 1980; Dubey, Speer and Epling, 1982).

Markus, Killick-Kendrick and Garnham (1974) considered that Dalmeny disease in Canadian cattle described by Corner et al. (1963) was due to *Sarcocystis* meronts. In this outbreak 25 cattle were affected; 5 of them died and 12 were killed when moribund; 10 of the 17 pregnant cows among them aborted. Small meronts indistinguishable in retrospect from those of *Sarcocystis* were found in the endothelial cells of the blood vessels of many organs in 11 out of 16 of the animals examined histologically. Meads (1976) reported another outbreak of Dalmeny disease in dairy cattle in Canada. Lainson (1972) found a similar organism in the liver and lungs of a heifer calf in England. It seems certain that Dalmeny disease and the English case were both due to *Sarcocystis*. Schmitz and Wolf (1977) reported a fatal case possibly due to *S. cruzi* in a 2-week-old calf in Oregon. Clegg, Beverley and Markson (1978) described a clinical disease of calves in England resembling Dalmeny disease associated with an organism, "possibly Sarcocystis," that they found. Frelier, Mayhew and Pollock (1979) found that naturally occurring *S. cruzi* infections killed 2 dairy heifers on a New York dairy farm and made 6 others ill.

Other outbreaks in cattle have been reported in New York state by Frelier (1977), by Giles et al. (1980) in Kentucky, by Dubey and Bergeron (1982) in Montana, and by Ferguson (1979, see Dubey, Speer and Epling, 1982), and Collery and Weavers (1981) in Ireland.

The disease in calves is due primarily to the second-generation tachyzoites (Dubey, Speer and Epling, 1982).

Immunology. Aryeetey and Piekarski (1976) considered the indirect immunofluorescent test (IIFT) reliable in detecting *Sarcocystis* infection.

Lunde and Fayer (1977) found that the indirect hemagglutination

titer of experimentally exposed cattle (against a *S. cruzi* soluble antigen prepared from bradyzoites in sarcocysts in the heart muscle) began to rise 30–45 days after inoculation and became as high as 1:39,000 90 days after inoculation. Because dairy cows from the field had titers as high as 1:486, they concluded that such titers were probably not significant for diagnosis. They also found precipitins in the gel diffusion test beginning 30 days after inoculation. They found no cross reaction in the IHA test between *S. cruzi* and *Toxoplasma gondii* with human sera.

Cross-Transmission Studies. Transmission from one predator to another by feeding sporocysts does not take place. It can occur only if the sporocysts are fed to the ox, or if ox tissues containing sarcocysts (not the earlier generations of meronts) are fed to the predators (Rommel et al., 1974; Fayer, 1974; Fayer and Johnson, 1975; Fayer, Johnson and Hildebrand, 1976; Dubey, 1980).

Animals that cannot be infected (or at least do not pass oocysts or sporocysts after having been fed bovine tissues infected with sarcocysts) are the cat (Gestrich, Heydorn and Baysu, 1975; Fayer, Johnson and Hildebrandt, 1976), skunk *Mephitis mephitis* (Fayer, Johnson and Hildebrandt, 1976), ferret *Mustela furo* (Fayer, Johnson and Hildebrandt, 1976), hyena *Crocuta crocuta* (Rommel et al., 1974), brown bear *Ursus arctos* (Rommel et al., 1974), pig (Fayer, Johnson and Hildebrandt, 1976), sheep (Gestrich, Schmitt and Heydorn, 1974; Gestrich, Heydorn and Baysu, 1975; Fayer, Johnson and Hildebrandt, 1976), rhesus monkey (Fayer, Johnson and Hildebrandt, 1976), laboratory rabbit (Fayer, Johnson and Hildebrandt, 1976), guinea pig (Suteu and Coman, 1973; Fayer, Johnson and Hildebrandt, 1976), laboratory mouse (Suteu and Coman, 1973), laboratory rat (Aryeetey and Piekarski, 1976; Fayer, Johnson and Hildebrandt, 1976) and chicken (Suteu and Coman, 1973).

Remarks. Leek and Fayer (1978) found *S. cruzi* in dogs fed raw or rare beef from a grocery store and a supermarket in Maryland, but not in dogs fed frozen meat, beef bologna or frankfurters. Fayer (1975) found that *S. cruzi* in ground beef hearts could survive refrigeration for 3 days and infect dogs. Cooked ground beef or ground beef frozen for 7 days could not infect dogs, although raw or rare ground beef could. Leek and Fayer (1979) found that *S. cruzi* sporocysts survived without appreciable deaths for over 300 days under refrigeration in distilled water or Hanks' balanced salt solution with

antibiotics, but that most were killed within a few days under refrigeration in 2% sulfuric acid, 2.5% potassium bichromate or 1% sodium hypochlorite solutions. They survived well at room temperature in distilled water in one experiment, and moderately well in a second experiment.

Mehlhorn, Heydorn and Gestrich (1975) recommended for control that meat be cooked at least until rosy, or that it be frozen for a long time at –20 C.

So far as is known, the sporocysts of this species cannot be distinguished from those of *S. tenella, S. miescheriana* or *S. bertrami,* which also occur in the dog.

Perhaps this is the species that Bigalke and Tustin (1960) found in the cerebellum of an ox in South Africa; that Luengo, Arata and Luengo (1974) found in the cerebellum of a heifer that died of tubercular meningoencephalitis in Chile; and that Munday and Black (1976) found in the brains of 2 bovine fetuses and the placentas of another 4 in Australia and New Zealand.

Amprolium (100 mg/kg for 30 days) reduces the severity of experimental *S. cruzi* sarcocystosis in calves (Fayer and Johnson, 1975).

Fayer and Leek (1979) found merozoites in the blood of experimentally infected calves and transmitted this species to other calves by blood transfusion.

Fayer, Leek and Lynch (1982) could not transmit *S. cruzi* from cows to calves via the colostrum.

S. cruzi is haploid except in the zygote stage (Overdulve and Cornelissen, 1982).

***Sarcocystis hirsuta* Moulé, 1888**

Synonyms. Miescheria cruzi Hasselmann, 1923 in part; *Sarcocystis fusiformis* Railliet, 1897 of Babudieri (1932) and *auctores* in part; *S. marcovi* Vershinin, 1975 in part; *S. bovifelis* Heydorn, Gestrich, Mehlhorn and Rommel, 1975; large form of *Isospora bigemina* from cats of Gestrich, Mehlhorn and Heydorn, 1975; *Endorimospora cruzi* (Hasselmann, 1926) Tadros and Laarman, 1976.

Type Definitive Host. Cat *Felis catus.*

Other Definitive Host. European wild cat *Felis silvestris.*

Type Intermediate Host. Ox *Bos taurus.*

Location. Gamonts, gametes, zygotes, oocysts and sporocysts in lamina propria of villi of small intestine of cats. First- and second-

generation meronts in blood vessels of various organs of ox. Sarcocysts in striated muscles of ox.

Oocyst Structure. Oocysts in lamina propria 12-17 x 11–14 (mean 15 x 12) μm in Giemsa-stained smears (Heydorn and Rommel, 1972); in intestinal scrapings 16–18 x 11–14 (mean 17 x 13) μm (Dubey, 1982a); smooth, colorless, presumably l-layered wall, without micropyle, residuum or polar granule. Oocyst wall stretched between the 2 sporocysts, producing a dumbbell-like appearance. Sporocysts with smooth wall thicker than that of the oocyst, 11–14 x 7–10 (mean 12.5 x 8) μm (Heydorn and Rommel, 1972; Rommel et al., 1974; Gestrich, Heydorn and Baysu, 1975; Dubey, 1982a; Suteu and Coman, 1973). Sporozoites 7.5–9 x 1.5–2 (mean 8 x 2) μm, with an anterior pointed end (Dubey, 1982a).

Merogony. There are 2 meront generations in cattle.

Dubey (1982a) found sporozoites in cattle within leukocytes in the lumen of arteries associated with mesenteric lymph nodes and intestine and in the mesenteric lymph nodes themselves. He found first-generation meronts 7–23 days after inoculation (DAI) in arteries associated with the mesenteric lymph nodes and intestine and in the mesenteric lymph nodes themselves. They matured 7–10 DAI, at which time they were 37 x 22 μm and contained more than 100 tachyzoites 5 x 1 μm. He found second-generation meronts in the capillaries of the heart and also of the thigh, diaphragm, tongue and eye muscles 15–23 DAI. They matured 15–16 DAI, at which time they were 14 x 6.5 μm and contained 3–35 merozoites 4 x 1.5 μm. Sarcocysts have been found in the striated muscles of cattle fed sporozoites or sporocysts from cats that had been fed raw esophageal muscle from cattle. Gestrich, Mehlhorn and Heydorn (1975) found them in calves 98 days after being fed sporozoites; they were always within a muscle fiber and never surrounded by fibrillar layers of host origin. They were limited by a single unit membrane thickened at many places by osmiophilic material. This primary wall was up to 24 nm thick and folded regularly to form palisade-like protrusions about 5 μm long and 1.5 μm in diameter. These protrusions contained about 200–300 parallel fibrils about 15–18 nm in diameter running from their tip into the interior of the sarcocyst. At this time there were both metrocytes and merozoites in chamber-like hollows of the ground substance of the sarcocysts. The metrocytes formed merozoites; by 120 days only merozoites were present. The sarcocyst wall was up to

5.4 μm thick and appeared radially striated by light microscopy (Heydorn et al., 1975). In other words, it is much thicker than that of *S. cruzi*. Dubey (1982a) found sarcocysts 25–75 DAI in the striated muscles, but not in the heart; they were most common in the esophageal muscles. At first they contained only metrocytes, then metrocytes and bradyzoites, and finally bradyzoites alone. When mature they were up to 800 μm long and had a striated wall up to 6 μm thick. They became infective for cats 75 DAI.

The metrocytes are globular, about 12–14 x 5–7 μm, with a typical 3-layered pellicle, deep micropores, a conoid, polar ring with 22 anchored subpellicular microtubules, and very few rhoptries and micronemes.

The bradyzoites are about 13–17 x 2.5–3 μm and have 22 subpellicular microtubules, normally 1 micropore at the apical pole, several rhoptries (12 in single longitudinal sections), and numerous micronemes filling the anterior third of the cell. They also have all of the other organelles of other coccidia.

Gamogony. Sheffield and Fayer (1978) found that the oocysts develop *extra*cellularly in the lamina propria of the cat small intestine. Heydorn and Rommel (1972) first found developmental stages in the cat 6 hours after feeding microscopic sarcocysts from the esophagus of cattle. They were rounded and in the lamina propria under the epithelium of the villi of the whole small intestine. After 3 days live macrogametes there were 11–14 x 8–9 (mean 12.5 x 8) μm. After 5 days oocysts in the lamina propria were 12–17 x 11–14 (mean 15 x 12) μm. They saw no microgamonts or meronts.

Prepatent Period. Seven to 10 or more days (Markus et al., 1974; Rommel et al., 1974; Gestrich, Heydorn and Baysu, 1975; Rybaltovskii, Dudkina and Rubina, 1973; Dubey and Streitel, 1976; Dubey, 1982a; Wolters, Heydorn and Laudahn, 1980).

Patent Period. 6 days to more than 6 weeks (Dubey and Streitel, 1976; Heydorn and Rommel, 1972; Rommel et al., 1974; Gestrich, Heydorn and Baysu, 1975; Suteu and Coman, 1973).

Pathogenicity. This species is nonpathogenic or only slightly so, for calves. Calves fed 2 million sporocysts had little or no clinical reaction (Gestrich, Heydorn and Baysu, 1975), and Dubey (1983) found that some but not all newborn calves fed 1–25 million sporocysts developed fever, anemia and diarrhea 11–30 days later, but none died.

S. hirsuta is apparently nonpathogenic for the cat.

Cross-Transmission Studies. So far as is known, only cats pass sporocysts or oocysts after oral inoculation. The following have been found not to do so: laboratory mouse and guinea pig (Suteu and Coman, 1973), laboratory rat (Aryeetey and Piekarski, 1976), rhesus monkey *Macaca mulatta* and baboon *Papio cynocephalus* (Heydorn, Gestrich and Janitschke, 1976), splenectomized chimpanzee *Chimpansee troglodytes* (Markus et al., 1974), chicken (Suteu and Coman, 1973; Rybaltovskii, Dudkina and Rubina, 1973; Lane and Levine, unpublished).

Remarks. Gestrich (1974) found that the sarcocysts of *S. hirsuta* in bovine diaphragms were killed by storage for 3 days at –20 C or by heating to 65–70 C for 10 minutes. Gestrich and Heydorn (1974) found that the sarcocysts were still infectious for cats after 18 days at 2 C but not after 3 days at –20 C; in steaks they were killed only if the meat had been heated to an internal temperature of 65–70 C. They were still infectious in medium-done steaks.

Sarcocystis hominis (Railliet and Lucet, 1891) Dubey, 1976

Synonyms. Coccidium bigeminum var. *hominis* Railliet and Lucet, 1891; *Miescheria cruzi* Hasselmann, 1923 in part; *Isospora hominis* (Railliet and Lucet, 1891) Wenyon, 1923; *Lucetina hominis* (Railliet and Lucet, 1891) Henry and Leblois, 1926; *Sarcocystis fusiformis* Railliet, 1897 of Babudieri (1932) and *auctores* in part; *Sarcocystis bovihominis* Heydorn, Gestrich, Mehlhorn and Rommel, 1975; *Endorimospora hominis* (Railliet and Lucet, 1891) Tadros and Laarman, 1976.

Type Definitive Host. Man *Homo sapiens.*

Other Definitive Hosts. Rhesus monkey *Macaca mulatta,* baboon *Papio cynocephalus,* chimpanzee *Chimpansee troglodytes* (?).

Type Intermediate Host. Ox *Bos taurus.*

Location. Sexual stages in the small intestine of man and the other primate hosts. Location of early meronts (if any) unknown. Sarcocysts in striated muscles of ox.

Oocyst Structure. Oocysts sporulated when passed, about 20 x 15 μm, with very thin, smooth wall stretched around the sporocysts and usually constricted between them to form a dumbbell-shaped structure, wall sometimes not visible, often ruptured, releasing the sporocysts. Oocysts without micropyle, residuum or polar granule. Sporocysts ellipsoidal or with one side flattened, about 12–16 x 8–12 μm (Wonde and Akao, 1973; Rommel and Heydorn, 1972; Gestrich,

Heydorn and Baysu, 1975; Heydorn, Gestrich and Janitschke 1976) without Stieda body, with residuum.

Merogony. There are probably 1 or 2 meront generations such as occur in *S. cruzi* in the endothelial cells of cattle, but they apparently have not been seen if they exist. Sarcocysts in the striated muscles of cattle are compartmented, with a thick, striated wall 6 μm thick, with many fibrils which resemble those of *S. hirsuta.* They resemble the sarcocysts of *S. hirsuta* (see above) with certain differences. The metrocytes are 6–7 x 4.5 μm and the bradyzoites 7–9 μm long. The latter have few micronemes, and these are only at the periphery; there are only 6–8 rhoptries in a longitudinal section. Like *S. cruzi* and *S. hirsuta,* however, they have 22 subpellicular microtubules (Gestrich, Mehlhorn and Heydorn, 1975; Heydorn, Mehlhorn and Gestrich, 1975).

Prepatent Period. 8–10 days (Gestrich, Heydorn and Baysu, 1975; Rommel and Heydorn, 1972).

Patent Period. More than 6 weeks or as long as 21 months (Gestrich, Heydorn and Baysu, 1975; Rommel and Heydorn, 1972; Laarman, 1963).

Pathogenicity. This species does not appear to be pathogenic for cattle, but it apparently is for man. Most human infections appear to be subclinical and self-limiting. However, *S. hominis* may cause a mucous diarrhea. In 31 of 33 cases of *Sarcocystis* or Isospora infection studied by Barksdale and Routh (1948), anorexia, nausea, abdominal pain and diarrhea were present. Wonde and Akao (1973) said that some infected persons in Ethiopia had colicky abdominal pain, loss of appetite, discomfort and diarrhea. Janitschke (1974) said that 6 out of the 12 infected persons he saw in Germany had various gastrointestinal symptoms.

Immunity. There is no serologic cross-reaction between *Toxoplasma gondii* and *Sarcocystis hominis* (Markus, 1973, 1974; Doby and Beaucournu, 1972). Tadros, Laarman and van den Eijk (1974) found that the indirect immunofluorescence test, using smeared cysts of *S. "fusiformis"* from cattle, was positive with the sera of 6 persons carrying *S. hominis* and of the donor cow, but negative with sera from a pathogen-free mouse, a *Toxoplasma*-infected mouse, and four 3–6-month-old babies.

Cross-Transmission Studies. The rhesus monkey *Macaca mulatta* and baboon *Papio cynocephalus* were infected with *S. hominis* by Heydorn,

Gestrich and Janitschke (1976). Rijpstra (1967) found what may have been this species in a pet chimpanzee in the Netherlands; its owner was infected with *S. hominis*. The dog and cat cannot be infected by ingesting infected bovine muscle or sporocysts (Rommel, 1975; Elsdon-Dew, 1954).

***Sarcocystis* spp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Ox *Bos taurus*.

Location. Cerebellum.

Merogony. Bigalke and Tustin (1960) found a single sarcocyst in the cerebellum of an ox in South Africa. It was septate, ellipsoidal, 142 x 77 μm in a section of the brain, and had no nuclei in its wall. The sarcocyst wall was smooth and less than 1 μm thick. There was no cellular reaction. The bradyzoites were spherical, ovoid, ellipsoidal or banana-shaped, the last being 9–10 x 3–4 (mean 10 x 3) μm.

Remarks. Munday and Black (1976) found *Sarcocystis* sp. meronts in the brains of 2 aborted bovine fetuses and the placentas of another 4 in Australia. They were mainly in endothelial cells of the blood vessels. Those in the brain were 18–35 x 13–16 (mean 26 x 15) μm. They also found possible metrocytes about 17 μm in diameter in endothelial cells of cerebral capillaries. Pass (1977) found what was probably *Sarcocystis* sp. and either *Sarcocystis* sp. or *Toxoplasma gondii* in the brains of aborted calves in Australia.

***Sarcocystis* sp. Welch and Zimmer, 1981**

Type Definitive Host. Unknown.

Type Intermediate Host. Gaur *Bos gaurus*.

Location. Striated muscles. The sarcocysts were in the esophageal muscles of one gaur and the myocardium of another.

Prevalence. Welch and Zimmer (1981) found this form in 2 of 3 gaurs born in the Oklahoma City Zoo that had died of African malignant catarrhal fever.

Oocyst Structure. Unknown.

Sporulation. Unknown.

Merogony. Welch and Zimmer (1981) said that the largest sarcocysts in the gaurs were 163 x 81 μm and contained banana-shaped bradyzoites 10 x 2 μm. The sarcocyst wall was thin (1.5–2.5 μm thick), without septa.

***Toxoplasma gondii* (Nicolle and Manceaux, 1908) Nicolle and Manceaux, 1909**

Synonyms. See Levine, 1977.

Type Definitive Host. Domestic cat *Felis catus.*

Other Definitive Hosts. Jaguarundi *Felis yagouaroundi,* ocelot *F. pardalis,* mountain lion *F. concolor,* Asian leopard cat *F. bengalensis,* bobcat *Lynx rufus,* probably cheetah *Acinonyx jubatus.*

Type Intermediate Host. Gondi *Ctenodactylus gundi.*

Other Intermediate Hosts. Over 200 species of mammals (including *Bos taurus* and felids) and birds known.

Location. One type of meront, gamonts, gametes, zygotes and oocysts in epithelial cells of villi of small intestine of the cat and other felids. Other meronts and merozoites in many types of cell of intermediate hosts, including neurons, microglia, endothelium, hepatocytes, lung and glandular epithelial cells, cardiac and skeletal muscle cells, fetal membranes and leukocytes. In acute infections, merozoites may be found free in the blood and peritoneal exudate. Merozoites normally occur in the cytoplasm of host cells, but may on rare occasions invade the nucleus, at least in tissue culture cells.

For other information see Levine and Ivens (1981) and Levine (1973).

Pathogenicity. The disease caused by *T. gondii* in cattle may vary considerably in its manifestations. Cows may develop nervous signs and die. Adult animals may have anorexia, diarrhea, weakness, ataxia, fever, mastitis, depression, prostration, chewing movements and bicycling; they may even die. Calves may be born dead or may die between the ages of 1 day and 6 months with signs of dyspnea, coughing, sneezing, nasal discharge, frothing at the mouth, trembling, headshaking, dehydration and occasionally diarrhea with blood and mucus (Senger et al., 1953; van der Wouden, 1961; Munday, Mason and Cummings, 1973; Pass, 1977; Ferguson and Ellis, 1979). (Some workers believe that at least some of these infections were due to *Sarcocystis*).

For additional information, see Levine (1973).

***Toxoplasma bahiensis* (de Moura Costa, 1956 emend. Levine, 1978) Levine, 1983**

Synonyms. Isospora bigemina (Stiles, 1891) Lühe, 1906 of *auctores;* [*non*] *I. bigemina* (Stiles, 1891) Lühe, 1906; *I. bigemina* Stiles, 1891 var.

bahiensis de Moura Costa, 1956 emend. Levine, 1978; *I. wallacei* Dubey, 1976; *I. heydorni* Tadros and Laarman, 1976; *Hammondia heydorni* (Tadros and Laarman, 1976) Dubey, 1977; *Toxoplasma heydorni* (Tadros and Laarman, 1976) Levine, 1977.

Type Definitive Host. Dog *Canis familiaris.*

Other Definitive Host. Coyote *C. latrans.*

Type Intermediate Host. Ox *Bos taurus.*

Other Intermediate Hosts. Sheep *Ovis aries,* goat *Capra hircus,* moose *Alces alces,* guinea pig *Cavia porcellus,* dog *Canis familiaris.* Matsui et al. (1981) could not infect the mouse, rat, hamster or rabbit.

Transport Hosts. Guinea pig, dog (Matsui et al., 1981).

Location. Oocysts and sporocysts in feces of definitive hosts; meronts and merozoites in muscles and presumably viscera of intermediate hosts.

Oocyst Structure. Spherical or subspherical, 10–14 x 10–12 (mean 12 x 10) μm, with smooth, colorless, 1-layered wall 0.4 μm thick; after sporulation without micropyle or residuum, with polar granule initially but disappearing after sporulation and storage. Sporocysts broadly ellipsoidal, 7–8 x 5–7 (mean 8 x 6) μm, without Stieda body, with residuum. Sporozoites banana- or sausage-shaped, pale, without clear globule.

Prepatent Period. 3–10 days in dog, 6 days in coyote (Heydorn, 1973; Dubey, 1980).

Patent Period. 5–9 days in dog, 5 days in coyote (Heydorn, 1973; Dubey and Fayer, 1976).

Pathogenicity. Dubey (1980) found no evidence of pathogenicity in lightly infected dogs, coyotes, sheep, goats or moose.

Immunity. Heydorn (1973) said that dogs that had been previously infected with this species were not resistant to reinfection 6 or more weeks later. He found that the Sabin-Feldman dye test for *Toxoplasma gondii* antibodies was negative with the sera of infected dogs. Cross-reactions occur between this species and *T. gondii* (see Araujo, Dubey and Remington, 1984).

***Besnoitia besnoiti* (Marotel, 1913) Henry, 1913**

Synonyms. Sarcocystis besnoiti Marotel, 1913; *Gastrocystis besnoiti* (Marotel, 1912) Brumpt, 1913; *Gastrocystis robini* Brumpt, 1913; *Glo-*

bidium besnoiti (Marotel, 1912), Wenyon, 1926; *Isospora besnoiti* (Marotel, 1912) Tadros and Laarman, 1976.

Type Definitive Host. Cat *Felis catus.*

Other Definitive Host. Wild cat *Felis libyca.*

Type Intermediate Host. Ox *Bos taurus.*

Other Intermediate Hosts. Zebu *Bos indicus,* blue wildebeest *Connochaetes taurinus,* impala *Aepyceros melampus,* kudu *Tragelaphus strepsiceros,* domestic goat *Capra hircus,* wild goat *C. aegagrus,* and experimentally domestic sheep *Ovis aries,* domestic rabbit *Oryctolagus cuniculi,* guinea pig *Cavia porcellus,* golden hamster *Mesocricetus auratus,* ground squirrel *Spermophilus fulvus,* marmot *Marmota* sp., house mouse *Mus musculus* and gerbil *Meriones* sp. (Bwangamoi, 1968; McCully et al., 1966; Pols, 1954, 1960; Neuman, 1962a; Neuman and Noble, 1963; Bigalke, 1968; Peteshev, Polomoshnov and Eshtokina, 1975; Peteshev, Galuzo and Polomoshnov, 1974; Rommel, 1975; Neuman, Nobel and Perelman, 1979).

Location. Gamonts, gametes, zygotes, oocysts, and probably last-generation meronts presumably in intestine of felids. Meronts in the cutis, subcutis, scleral conjunctiva, connective tissue, fascia, serosae, mucosae of the nose, larynx, trachea, vaginal mucosa, endometrium, and other places of intermediate hosts. Merozoites in the blood, either extracellularly or in monocytes, and in smears of lymph nodes, lungs, testes, etc., of intermediate hosts.

Prepatent Period. 4–25 days.

Patent Period. 3–15 days.

Pathogenicity. B. besnoiti is apparently not pathogenic for the cat definitive host. However, it may cause serious disease in the bovine intermediate host. The antelope reservoirs do not appear to be severely affected. Most infected cattle have low grade, chronic infections without skin lesions. The typical signs in clinically affected cattle are anasarca followed by scleroderma, alopecia and seborrhea (Bigalke and Naudé, 1962). The most complete description of clinical bovine besnoitiosis was given by Hofmeyr (1945) and quoted in part by Levine (1973). There are 3 stages in the course of the disease. In the febrile stage there is fever first, followed by photophobia and anasarca. In the depilatory stage the skin is thick and the hair falls out. Hard sitfasts develop where the animal contacts the ground when it lies down. If the animal does not die, it passes to the seborrhea sicca

stage, in which the hide resembles elephant skin and the animal looks as though it has mange. The lymph nodes are permanently enlarged, the protozoan pseudocysts remain, and the animal is listless and debilitated.

In light infections in which little hair has been lost, the animals become practically normal in appearance, but in more severe cases recovery takes months or years.

Herd morbidity is 1–20%, and mortality is about 10%.

In the acute stage degenerative and necrotic lesions, vasculitis and thrombosis, mainly of the medium-sized and smaller veins and some arteries occur. These coincide with parasitization of endothelial and other cells of the vessels, where the organisms multiplied before the beginning of the last meront (pseudocyst) stage. These basic lesions are responsible for edema, degenerative changes and even infarction, particularly in the testes and skin. Other characteristic features are a histiocytic reaction and mild eosinophil infiltration.

The pseudocyst stage in cattle apparently develops in enlarged histiocytes, and can be recognized 11 days after inoculation. The host cells become multinuclear and form the pseudocyst wall. The pseudocysts become mature 71 days after inoculation (Basson, McCully and Bigalke, 1970).

Bovine strains are markedly pathogenic, causing severe testicular or skin lesions. Wildebeest and impala strains are only mildly pathogenic for rabbits, but passage during the acute stage increases their pathogenicity (Basson, McCully and Bigalke, 1970).

Marmots die of besnoitiosis 10–12 days after having been inoculated with material from cattle. Sheep and goats have a temperature which begins 10–13 days after inoculation and lasts 3–9 days. It then declines, and the animals remain clinically healthy (Peteshev, Galuzo and Polomoshnov, 1974).

B. besnoiti may cause central nervous system signs (choreiform head movements, irritability, hypersensitivity, weakness, especially of the hind legs, ataxia and later on paraplegia and death in experimentally inoculated rabbits, golden hamsters, guinea pigs, gerbils and white mice) (Neumann, Nobel and Perleman, 1979).

Immunity. Animals infected with *B. besnoiti* are positive to the complement fixation test (Peteshev, Galuzo and Polomoshnov, 1974), the indirect fluorescence antibody and the ELISA (peroxidase) tests (Wei-

land and Kaggwa, 1976). There is no cross-reaction with *Toxoplasma gondii.*

Bigalke et al. (1973) and Bigalke, Schoeman and McCully (1974) immunized cattle and rabbits against *B. besnoiti* by use of a live vaccine prepared from a strain from the blue wildebeest grown in tissue culture.

Remington (1969) found that infection of mice with *B. besnoiti* protected them against *Listeria monocytogenes, Salmonella typhimurium, Brucella melitensis, Plasmodium berghei, Toxoplasma gondii* and Mengo virus. He considered that common mechanisms of intracellular immunity exist, and that the macrophage system is the effector arm of the observed resistance.

Cross-Transmission Studies. Only *Felis catus* and *F. libyca* have so far been found to produce oocysts. Known animals in which oocysts are not produced are the intermediate hosts and the dwarf vulture *Pseudogyps africanus,* maribou stork *Leptoptilus crumeniferus* (Rommel, 1975), wolf, corsac fox, hedgehog, and rook (Peteshev, Galuzo and Polomoshnov, 1974).

Cultivation. B. besnoiti can be readily cultivated in tissue culture (Bigalke, 1962; Neuman, 1974; Akinchina and Doby, 1969; Bigalke, Schoeman and McCully, 1974).

Remarks. Pols (1960) and Bigalke (1968) reviewed bovine besnoitiosis.

See also the discussion of this species under *Connochaetes taurinus* below.

For other information see Levine and Ivens (1981) and Levine (1973).

Host Genus *Syncerus*

Sarcocystis spp.

Sarcocysts have been found in the striated muscles of the African buffalo *Syncerus caffer* in East Africa by Sachs and Sachs (1968), Kaliner et al. (1971), Kaliner, Grootenhuis and Protz (1974) and Kaliner (1975). Sachs and Sachs (1968) said that the sarcocysts they found were 50 x 20 mm or larger. Kaliner, Grootenhuis, and Protz (1974) found macrocysts and microcysts in 3 out of 4 animals.

Host Genus *Bison*

***Eimeria auburnensis* Christensen and Porter, 1939**

Ryff and Bergstrom (1975) said that they had found this species in the American bison *Bison bison* in Wyoming. See above under *Bos* for further information.

***Eimeria bovis* (Züblin, 1908) Fiebiger, 1912**

Yakimoff (1935b) reported this species from the wisent or European bison *Bison bonasus,* and Ryff and Bergstrom (1975) from the American bison *Bison bison* in Wyoming. These last said that *E. bovis* was the most common bovine species in the bison. See above under *Bos* for further information.

***Eimeria brasiliensis* Torres and Ramos, 1939**

Ryff and Bergstrom (1975) reported this species from the American bison *Bison bison* in Wyoming. See above under *Bos* for further information.

***Eimeria canadensis* Bruce, 1921**

Yakimoff (1935a) reported this species from the wisent or European bison *Bison bonasus,* and Ryff and Bergstrom (1975) from the American bison *Bison bison* in Wyoming. See above under *Bos* for further information.

***Eimeria ellipsoidalis* Becker and Frye, 1929**

Yakimoff (1935b) reported this species from the wisent or European bison *Bison bonasus* in the USSR. See above under *Bos* for further information.

***Eimeria zuernii* (Rivolta, 1878) Martin, 1909**

Yakimoff (1935) reported this species from the wisent or European bison *Bison bonasus* in the USSR. See above under *Bos* for further information.

***Sarcocystis* spp.**

Ippen et al. (1974) found sarcocysts in 2 out of 10 bison (specific name not given) in East Germany. Sarcocysts have been found in the American bison *Bison bison* (Mahrt and Colwell, 1980; Dubey, 1980;

and Fayer Dubey and Leek, 1982). Its definitive host is the coyote, and it causes signs in buffaloes similar to those caused by *S. cruzi* in the ox.

Host Genus *Cephalophus*

***Eimeria cephalophi* Pampiglione, Ricci-Bitti and Kabala, 1973**
(Fig. 311)

Type Host. Forest duiker *Cephalophus monticola.*

Oocyst Structure. Ellipsoidal to ovoid, 20–25 x 13–17 (mean 22 x 16) μm, with smooth, yellowish, 1-layered wall about 1 μm thick, with micropyle, without residuum or polar granule. Sporocysts ellipsoidal, 12 x 5 μm, without Stieda body, with residuum. Sporozoites comma-shaped, lying lengthwise head to tail in sporocysts, presumably without clear globules.

***Eimeria iturina* Pampiglione, Ricci-Bitti and Kabala, 1973**
(Fig. 312)

Type Host. Forest duiker *Cephalophus monticola.*

Oocyst Structure. Ellipsoidal, 19–26 x 16–21 (mean 23 x 18) μm, with 2-layered wall about 2 μm thick with layers that can be separated with difficulty, outer layer rough, brown, thinning toward anterior end until it disappears, inner layer smooth, colorless, apparently without micropyle, without residuum or polar granule. Sporocysts ellipsoidal, 14 x 7 μm, with Stieda body and residuum. Sporozoites comma-shaped, lying lengthwise head to tail in sporocysts, with 2 clear globules each.

***Eimeria turnbulli* Pampiglione, Ricci-Bitti and Kabala, 1973**
(Fig. 319)

Type Host. Forest duiker *Cephalophus dorsalis.*

Other Hosts. Forest duikers *Cephalophus monticola, C. nigrifrons.*

Oocyst Structure. Ovoid, 23–38 x 20–27 (mean 32 x 23) μm, with 2-layered wall about 2 μm thick, outer layer rough, brown, easily separated from inner layer, which is smooth and colorless, with micropyle in outer but not inner layer, without residuum or polar granule. Sporocysts elongate ovoid, 16 x 6 μm, with Stieda body and residuum. Sporozoites comma-shaped, lying lengthwise head to tail in sporocysts, generally with 2 or more clear globules each.

Host Genus *Sylvicapra*

***Sarcocystis* sp.**

Thils, Déom and Fagard (1960), Keymer (1969), Kaliner et al. (1971) and Kaliner (1975) found *Sarcocystis* sarcocysts in the striated muscles of the duiker *Sylvicapra grimmia* in Africa.

Host Genus *Kobus*

***Eimeria congolensis* Ricci-Bitti, Pampiglione and Kabala, 1973**
(Fig. 318)

Type Host. Waterbuck *Kobus defassa.*

Oocyst Structure. Ovoid, 27–33 x 19–24 (mean 30 x 22) μm, with rough, brown, 2-layered wall about 1.5 μm thick, with layers easily separated, outer layer finely granular, brown, inner layer smooth, colorless, with micropyle in outer layer only, without residuum or polar granule. Sporocysts ellipsoidal, with a pointed end, 14 x 7 μm, sometimes with 2 granules which may be a residuum, with very small, hardly visible Stieda body. Sporozoites lying lengthwise head to tail in sporocysts, with 1 or more clear globules each.

***Eimeria dathei* Tscherner, 1976**

Type Host. Waterbuck *Kobus ellipsiprymnus.*

Oocyst Structure. Ovoid or ellipsoidal, somewhat flattened at micropylar end, 52–59 x 35–39 μm, with 3-layered wall, outer layer granular, dark brown, 3 μm thick, middle layer transparent; inner layer very dark, thin; middle and inner layers together about 3 μm thick, with micropyle 10 μm in diameter, without micropylar cap, without residuum. Sporocysts spindle-shaped, 28 x 10 μm, with Stieda body and residuum. Oocyst does not rise in concentrated NaCl solution and is found in the sediment.

***Eimeria katangensis* Ricci-Bitti, Pampiglione and Kabala, 1973**
(Fig. 320)

Type Host. Waterbuck *Kobus defassa.*

Oocyst Structure. Ovoid, 34–44 x 22–26 (mean 41 x 25) μm, with smooth, brown, 1-layered wall about 2 μm thick, with micropyle, without residuum or polar granule. Sporocysts ellipsoidal with pointed ends, 20 x 7.5 μm, with a small Stieda body and residuum.

Sporozoites comma-shaped, lying lengthwise head to tail in sporocysts, with several clear globules each.

***Eimeria kobi* Ricci-Bitti, Pampiglione and Kabala, 1973** (Fig. 317)

Type Host. Waterbuck *Kobus defassa.*

Oocyst Structure. Ellipsoidal, 34–41 x 26–30 (mean 38 x 28) μm, with rough, brown, 2-layered wall about 2 μm thick, outer layer granular, brown, easily detachable from the inner layer, which is smooth and colorless, with micropyle in outer layer, not visible in inner one, without residuum or polar granule. Sporocysts ellipsoidal, 21 x 8 μm, with Stieda body and residuum. Sporozoites comma-shaped, with several clear globules each.

***Eimeria macieli* Yakimoff and Matchulski, 1938**
(Fig. 59, Levine and Ivens, 1970)

Type Host. Waterbuck *Kobus* (syn., *Cobus) ellipsiprymnus.*

Oocyst Structure. Ovoid, flattened at micropylar end, 24–34 x 20–24 (mean 30 x 21) μm, with double-contoured, radially striated wall 1.5 μm thick, with micropyle, without residuum or polar granule. Sporocysts described as ovoid, 10–14 x 4–6 μm, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts.

***Eimeria* sp. Ricci-Bitti, Pampiglione and Kabala, 1973**

Type Host. Waterbuck *Kobus defassa.*

Oocyst Structure. Subspherical, 16–20 x 14–18 (mean 18 x 16) μm, with smooth, colorless, 1-layered wall about 1 μm thick, with micropyle present as a thinning of the wall, with residuum, without polar granule. Sporocysts ellipsoidal, 10 x 5 μm.

***Sarcocystis nelsoni* Mandour and Keymer, 1970**

Type Definitive Host. Unknown.

Type Intermediate Host. Defassa waterbuck *Kobus defassa.*

Location. Sarcocysts in striated muscles.

Merogony. Muscle meronts (sarcocysts) 5 x 1.5 mm. (Sachs and Sachs, 1968, found sarcocysts 20–30 x 2–4 mm; Kaliner, Grootenhuis and Protz, 1974, found macrocysts only). Muscle merozoites (bradyzoites) from sarcocysts 10–13 x 2–3 μm in sections, 14–16 x 2–3 μm in fixed smears.

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Common waterbuck *Kobus ellipsiprymnus.*

Location. Striated muscles.

Merogony. Mandour and Keymer (1970) found merozoites in the blood 11–20 x 2.5 (mean 16 x 4) μm.

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Uganda kob *Kobus (Adenota) kob.*

Location. Striated muscles (Brocklesby and Vidler, 1966; Kaliner et al., 1971).

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Puku *Kobus vardoni.*

Location. Striated muscles.

Merogony. Mandour and Keymer (1970) found merozoites 15 x 5 μm in the blood in Zambia.

Host Genus *Redunca*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Bohor reedbuck *Redunca redunca.*

Location. Striated muscles (Kaliner, Grootenhuis and Protz, 1974).

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Reedbuck *Redunca* (syn., *Cervicapra arundinum.*

Location. Striated muscles, heart (Fantham, 1921; Viljoen, 1921).

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Chandler's mountain reedbuck *Redunca chanleri.*

Location. Striated muscles (Kaliner, Grootenhuis and Protz, 1974).

Host Genus *Damaliscus*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Topi *Damaliscus korrigum.*

Location. Striated muscles.

Merogony. The sarcocysts seen by Sachs and Sachs (1968) were 40 x 1 mm.

Host Genus *Alcelaphus*

***Eimeria talboti* Prasad and Narayan, 1963**

(Fig. 196, Levine and Ivens, 1970)

Type Host. Hartebeest or kongoni *Alcelaphus cokei* (syn., *A. cockei).*

Oocyst Structure. Ovoid and asymmetrical, one side being slightly more convex than the other, 35–38 x 22–28 (mean 36 x 25) μm, with smooth, yellowish, 2-layered wall, without micropyle, residuum or polar granule. Sporocysts generally piriform, 12–15 x 9–10 (mean 14 x 10) μm, without Stieda body or residuum. Sporozoites spindle-shaped, lying lengthwise in sporocysts with both broad ends at the large end of the sporocyst, with large clear globule at the rounded end.

***Eimeria* sp.**

Type Host. Hartebeest or kongoni *Alcelaphus cokei* (syn., *A. cockei).*

Oocyst Structure. Ellipsoidal, 22–28 x 19–20 (mean 25 x 19) μm, with colorless, 2-layered wall with outer layer slightly thicker than inner one, without micropyle or residuum, with polar granule. Sporocysts lemon-shaped, 11–13 x 6–7 (mean 11 x 6) μm, with very thick wall and prominent Stieda body. Sporozoites with one end broadly rounded and the other sharply pointed.

Remarks. Prasad and Narayan (1963) found only a few oocysts of this form and therefore hesitated to name it.

***Sarcocystis bubalis* Dogel', 1916**

Type Definitive Host. Unknown.

Type Intermediate Host. Coke's hartebeest *Alcelaphus buselaphus cokii* (syn., *Bubalus cookei).*

Location. Striated muscles of intermediate host.

Merogony. Sarcocysts not compartmented, 0.25–2 mm x 65–200

μm, with cytophaneres. Bradyzoites in sarcocysts elongate, slightly bean-shaped, about 10 μm long.

***Sarcocystis* spp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Hartebeest or kongoni *Alcelaphus buselaphus.*

Location. Striated muscles of intermediate host (Kaliner, Grootenhuis and Protz, 1974).

Host Genus *Connochaetes*

***Eimeria connochaetei* Levine and Ivens, 1970**

(Fig. 197, Levine and Ivens, 1970)

Synonym. Eimeria ellipsoidalis Becker and Frye, 1929 of Prasad, 1960.

Type Host. Probably brindled gnu (blue wildebeest) *Connochaetes taurinus.*

Oocyst Structure. Roughly ellipsoidal, 20–27 x 13–15 (mean 22 x 14) μm, with smooth, pale yellow, 2-layered wall, without micropyle, residuum, or polar granule. Sporocysts ovoid, with small Stieda body and residuum. Sporozoites 4–5 x 1.5 μm, lying lengthwise in sporocysts, with clear globule at the large end.

Remarks. Prasad (1960) also said that the host was the white-tailed wildebeest, black wildebeest or gnu *Connochaetes gnou,* but W. von Richter (1971 *in litt.)* said that the host could not be this species because it does not and never did occur in East Africa, but is found in South Africa. He said that *C. taurinus* was probably meant, since the geographic distribution of this species includes East Africa.

***Eimeria gorgonis* Prasad, 1960**

(Fig. 203, Levine and Ivens, 1970)

Type Host. Brindled gnu (blue wildebeest) *Connochaetes* (syn., *Gorgon) taurinus.*

Oocyst Structure. Ellipsoidal, 20–26 x 15–18 (mean 23 x 16.5) μm, with smooth, 2-layered wall, outer layer pale yellow and slightly thicker than the colorless inner layer, without micropyle or residuum, with very small polar granule. Sporocysts lemon-shaped with a distinct neck, 12–15 x 4–6 μm, with prominent Stieda body and residuum, with a refractile vacuole at the narrow end and a double

membrane. Sporozoites club-shaped, 10–13 x 3 μm, lying lengthwise head to tail in sporocysts, with a clear globule at the large end.

***Besnoitia besnoiti* (Marotel, 1913) Henry, 1913**

Type Definitive Host. Cat *Felis catus.*

Other Definitive Host. Wild cat *Felis libyca.*

Type Intermediate Host. Ox *Bos taurus.*

Other Intermediate Hosts. Zebu *Bos indicus,* blue wildebeest *Connochaetes taurinus,* impala *Aepyceros melampus,* kudu *Tragelaphus strepsiceros,* goat *Capra hircus;* experimentally domestic sheep *Ovis aries,* domestic rabbit *Oryctolagus cuniculi,* guinea pig *Cavia porcellus,* golden hamster *Mesocricetus auratus,* ground squirrel *Spermophilus fulvus,* marmot *Marmota* sp. and house mouse *Mus musculus.*

Basson et al. (1965) and McCully et al. (1966) found whitish *B. besnoiti* cysts a little less than 0.5 mm in diameter attached to the endothelium and intima of the blood vessels of 19 of 21 blue wildebeests, 33 of 74 impalas, 1 of 6 kudus, and of cattle in Kruger National Park, South Africa. The antelopes had no clinical signs of disease. Bigalke et al. (1967) transmitted the blue wildebeest strain to rabbits and carried it thru 27 serial passages by subinoculation of blood. The rabbits' reactions were different from those to bovine strains. Skin lesions did not develop, and it was hard to find zoites in blood smears, but they were plentiful in the internal organs of fatal cases. The strain was very mild at first, but eventually became highly pathogenic for rabbits on continuous passage.

Cattle could be infected with the antelope strains but developed mild reactions. They were, however, immune to challenge.

Bigalke et al. (1967) infected sheep with a blue wildebeest strain. The sheep developed fairly severe reactions, but recovered. They had small numbers of cysts in the peripheral veins and nasal mucosa, but no zoites in blood smears.

The strains from the blue wildebeest, impala and cattle were mutually immunogenic, indicating that they were all the same species.

For further information on *B. besnoiti,* see the discussion above under *Bos.*

***Sarcocystis* spp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Blue wildebeest *Connochaetes taurinus.*

Location. Striated muscles of intermediate host (Sachs and Sachs,

1968; Brocklesby and Vidler, 1966; Kaliner et al., 1971; Kaliner, Grootenhuis and Protz, 1974; Kaliner, 1975).

Host Genus *Oreotragus*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Klipspringer *Oreotragus oreotragus.*

Location. Striated muscles of intermediate host (Viljoen, 1921).

Host Genus *Raphicerus*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Steenbock *Raphicerus capensis.*

Location. Striated muscles of intermediate host (Viljoen, 1921).

Host Genus *Madoqua*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Dik-dik *Madoqua* (syn., *Rhynchotragus) kirkii.*

Location. Striated muscles of intermediate host (Kaliner et al., 1971; Kaliner, 1975).

Host Genus *Antilope*

***Eimeria antilocervi* Ray and Mandal, 1960 emend. Levine and Ivens, 1970**

Synonym. Eimeria antelocervi Ray and Mandal, 1960.

Type Host. Presumably antelope *Antilope cervicapra;* Ray and Mandal (1960) called it *"Antelopecervi caprae."*

Oocyst Structure. Cylindrical, 28–34 x 12–16 μm, with light brown, presumably 1-layered wall 1.5–2 μm thick, with micropyle 1.5 μm in diameter, without residuum. Sporocysts piriform, 11 x 7 μm, with residuum.

Cross-Transmission Studies. Ray and Mandal (1960) were unable to transmit this species to a young calf (presumably a zebu calf).

***Eimeria mrigai* Pande, Chauhan, Bhatia and Arora, 1972** (Fig. 339)

Type Host. Blackbuck *Antilope cervicapra.*

Location. Oocysts and "some of the other endogenous stages" in villar epithelial cells of jejunum.

Oocyst Structure. Ellipsoidal or ovoid, 39–55 x 26–32 (mean 48.5 x 30) μm, with smooth, 2-layered wall about 2 μm thick, outer layer light yellowish green and 1.2–1.6 μm thick, inner layer yellowish-brown and 0.4–0.7 μm thick, with micropyle 5–8 μm in diameter, with prominent, transparent, somewhat helmet-shaped micropylar cap 13–18 x 2–3 μm, without residuum, with "tenue body" (polar body?) present as an irregularly-shaped clump of dark, large refractile granules just beneath the micropyle in both unsporulated and sporulated oocysts. Sporocysts ellipsoidal, 19–23 x 9–10 (mean 21 x 10) μm, with Stieda body and residuum. Sporozoites elongate, with one end pointed and the other broad, with a large clear globule at the broad end and 1–2 clear globules toward the other end.

Gamogony. The microgamonts and macrogametes are in the villar epithelial cells of the jejunum. Mature microgamonts are 33 x 31 μm and contain numerous rod-like microgametes 2–2.5 μm long. Mature macrogametes are 24–38 x 18–27 (mean 27.5 x 22) μm (Pande et al., 1972).

***Eimeria* sp. (Bhatia, 1968) nov. comb.**

Synonym. Eimeria cheetali Bhatia, 1968 in *Antilope cervicapra.*

Type Host. Blackbuck *Antilope cervicapra.*

Oocyst Structure. Ellipsoidal, 17–27 x 11–16 (mean 23 x 13.5) μm. The structural features of this species (except for the dimensions of the oocysts) are presumably the same as those of *E. cheetali.*

Remarks. Bhatia (1968) said that this species, named from the spotted deer *Axis axis,* also occurs in the blackbuck. However, this idea is extremely dubious, because *Axis* and *Antilope* are not only different genera but belong to different families.

Host Genus *Aepyceros*

***Eimeria impalae* Prasad and Narayan, 1963**
(Figs. 205, 206, Levine and Ivens, 1970)

Type Host. Impala *Aepyceros melampus.*

Location. Oocysts in feces. Endogenous stages in posterior third of jejunum and ileum, rarely in cecum and colon.

Oocyst Structure. Oocysts ellipsoidal, 30–36 x 20–24 (mean 33 x 22) μm, with a smooth, yellowish green, 2-layered wall, the inner layer slightly thicker than the outer, with micropyle, without residuum or polar granule. Sporocysts ovoid, 8–14 x 7–9 (mean 11 x 8) μm, without residuum, with or without Stieda body. Sporozoites spindle-shaped, 8–11 x 2–4 (mean 10 x 3) μm, with a clear globule at the broad, rounded end.

Gamogony. Bigalke (1964) found numerous gamonts, microgametes and oocysts in the small intestine and rarely in the cecum and colon. The mature macrogametes were about 21 x 17 μm. Both epithelial cells and histiocytes appeared to be parasitized. Microgamonts were in the same location as the macrogametes. They were 30–48 x 17–38 (mean 37 x 28) μm when mature. Microgametes developed in a number of nuclear whorls within the microgamonts; they became crescentic or filamentous and about 3–4 μm long when mature.

Pathogenicity. Pienaar et al. (1964) and Bigalke (1966) considered this species highly pathogenic when young impala were brought together in small paddocks. The most prominent sign is diarrhea. Numerous petechiae and suggilations 1 cm in diameter to 7 cm long involve the whole width of the gut, and the intestine is hyperemic.

The macrogametes, microgamonts, microgametes and oocysts are mainly in the epithelial cells lining the crypts of Lieberkuehn. The infected glands are greatly enlarged, and the blood vessels in the heavily infected part of the intestine are markedly congested. Occasionally small groups of organisms (mostly oocysts) occur in the lymph nodes in the submucosa just below the muscularis mucosae.

Remarks. It is possible that the form described by Bigalke (1964) may belong to a different species.

***Eimeria neitzi* McCully, Basson, de Vos and de Vos, 1970**

Type Host. Impala *Aepyceros melampus.*

Location. Oocysts, gamonts and gametes in cells of distal part of glands and adjacent surface epithelium of uterus.

Oocyst Structure. Spherical, subspherical or slightly ovoid, 29–34 x 28–33 (mean 32 x 30) μm, with smooth, colorless, 1-layered wall 0.5 μm thick, without micropyle or residuum, with polar granule in about 60%. Sporocysts ellipsoidal, tapering slightly toward one end,

16–19 x 6–8 (mean 17 x 7) μm, with small Stieda body at small end, and residuum. Sporozoites 10 μm long, rounded at one end and tapered at the other, lying lengthwise head to tail in sporocysts, with PAS-positive clear globule. Sporulation occurs in the host tissues.

Merogony. McCully et al. (1970) found no meronts or "authentic" merozoites.

Gamogony. Macrogametes, microgamonts and microgametes occur in the uterine glands. Mature microgamonts are up to 100 μm in diameter and contain many flagellated microgametes (McCully et al., 1970).

Pathogenicity. This coccidium apparently produces small intrauterine polyps and small white foci. It does not seem to have much if any effect on reproduction (McCully et al., 1970).

***Besnoitia besnoiti* (Marotel, 1913) Henry, 1913**

Type Definitive Host. Cat *Felis catus.*

Other Definitive Host. Wild cat *Felis libyca.*

Type Intermediate Host. Ox *Bos taurus.*

Other Intermediate Hosts. Zebu *Bos indicus,* impala *Aepyceros melampus,* blue wildebeest *Connochaetes taurinus,* kudu *Tragelaphus strepsiceros,* goat *Capra hircus* and various experimental hosts.

For further information, see the discussions above under *Bos* and *Connochaetes.*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Impala *Aepycerus melampus.*

Location. Striated muscles of intermediate host.

Merogony. The only sarcocysts that Kaliner, Grootenhuis and Protz (1974) found were microscopic (microcysts).

Host Genus *Litocranius*

***Eimeria walleri* Prasad, 1960**

(Fig. 204, Levine and Ivens, 1970)

Type Host. Gerenuk *Litocranius walleri.*

Oocyst Structure. Roughly ovoid, 27–30 x 22–25 (mean 28.5 x 23.5) μm, with smooth, colorless, 3-layered wall, with micropyle about 3 μm in diameter, without residuum or polar granule. Sporocysts

broadly ovoid, 8–13 x 5–8 μm with 2-layered wall, with very small Stieda body, with residuum. Sporozoites roughly club-shaped, lying lengthwise head to tail in sporocysts, with a clear globule at the large end.

Host Genus *Gazella*

***Eimeria abenovi* Svanbaev, 1979**

Synonym. Eimeria faurei (Moussu and Marotel, 1902) Martin, 1909 of Svanbaev (1969) in *Gazella subgutturosa.*

Type Host. Goitered gazelle *Gazella subgutturosa.*

Oocyst Structure. Ovoid, 23–41 x 19–26 (mean 32 x 22.5) μm, with smooth, "double-contoured," yellow-green wall 1.4–1.7 μm thick, with micropyle, without residuum or polar granule. Sporocysts ellipsoidal, 8–14 x 6–9 (mean 11 x 7) μm, without Stieda body, with residuum. Sporozoites 5–9 x 3–5 (mean 7 x 3.5) μm, apparently without clear globules.

Cross-Transmission Studies. Svanbaev (1979) failed to transmit this species from *G. subgutturosa* to 23 lambs.

***Eimeria chinkari* Pande, Bhatia, Chauhan and Garg, 1970** (Fig. 310)

Type Host. Gazelle or chinkara *Gazella gazella.*

Oocyst Structure. Subspherical, 24–27 x 19–26 (mean 25 x 22) μm, with smooth, 2-layered wall 1.3 μm thick, outer layer light greenish blue, inner layer dark yellowish blue, without micropyle, residuum, or polar granule. Sporocysts somewhat almond-shaped, 13–14 x 8–9 (mean 14 x 8) μm, with prominent plug-like Stieda body (substiedal body?) and residuum. Sporozoites presumably elongate, with one end broad and the other narrow, lying lengthwise head to tail in sporocysts, with a large and a small clear globule.

***Eimeria dorcadis* Mantovani, 1966**

(Fig. 207, Levine and Ivens, 1970)

Type Host. Gazelle *Gazella dorcas.*

Location. Feces.

Oocyst Structure. Ovoid or ellipsoidal, yellowish, 26–31 x 15–20 (mean 29 x 18) μm, with smooth, apparently 1-layered wall 1 μm thick, without micropyle, residuum or apparently polar granule. Sporocysts 21–26 x 8–11 (mean 23 x 9) μm, apparently without Stieda

body, with residuum. Sporozoites comma-shaped, 8–12 x 2–4 (mean 10 x 3) μm.

Cross-Transmission Studies. Mantovani (1966) was unable to transmit this species to a young goat or a young lamb.

***Eimeria elegans* Yakimoff, Gousseff and Rastegaieff, 1932**

Type Host. Goitered gazelle, zheiran or dscheiran *Gazella subgutturosa.*

Other Host. Gazelle *Gazella* sp.

Oocyst Structure. Elongate ovoid, almost cylindrical, with one end rounded and the other flattened, 23–45 x 16–25 μm, with smooth, 2-layered wall 1–2 μm thick, with micropyle, without residuum, with or without polar granule. Sporocysts ovoid, 10–14 x 6–12 μm, with residuum. Sporozoites bean-shaped, comma-shaped or piriform, 5–11 x 2–6 (mean 8 x 4.5) μm.

Cross-Transmission Studies. Yakimoff, Iwanoff-Gobzem and Matschoulsky (1936) were unable to infect a young goat with this species, and Svanbaev (1979) failed to transmit it to 23 lambs.

***Eimeria gazella* Musaev, 1970 emend. Svanbaev, 1979**

Synonyms. Eimeria ninakohlyakimovae Yakimoff and Rastegaieff, 1930 of Svanbaev (1958) in *Gazella subgutturosa.*

Type Host. Goitered gazella *Gazella subgutturosa.*

Oocyst Structure. Ovoid or spherical, 20–28 x 17–25 (mean 24 x 20) μm, with smooth, 2-layered wall 1–2 μm thick, with yellow-green and brown layers, without micropyle. Sporocysts ovoid to broad ovoid, 6–11 x 5–8 (mean 9 x 6) μm, with residuum. Sporozoites 4–8 x 2–4 (mean 6 x 3) μm.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species to 54 lambs.

***Isospora* sp.**

Mirza (1970) found *Isospora* sp. in the feces of 2 of 4 *Gazella* sp. in Iraq. He said that it was probably *I. lacazei* of sparrows.

***Sarcocystis gazellae* Balfour, 1913**

Type Definitive Host. Unknown.

Type Intermediate Host. Red-fronted gazelle *Gazella rufifrons.*

Location. Sarcocysts in striated muscles of intermediate host.

Merogony. Sarcocysts averaged 4 mm long. They contained crescent- or sickle-shaped merozoites 15–17 x 3–3.5 μm (when fixed and stained with Giemsa), and also apparently metrocytes.

Remarks. It is possible that *S. woodhousei* Dogel', 1916 from *G. granti* is a synonym of this species. However, see the Remarks under that species and under *Sarcocystis* sp. from *G. granti.*

***Sarcocystis mongolica* Machul'skii, 1947**

Type Definitive Host. Unknown.

Type Intermediate Host. Mongolian gazelle *Gazella gutturosa.*

Location. Striated muscles of intermediate host.

Merogony. Bradyzoites in sarcocysts 12–18 x 3–5 (mean 14 x 4) μm (Kalyakin and Zasukhin, 1975).

Remarks. We have not seen the paper in which this species was named and depend upon Kalyakin and Zasukhin (1975) for a report of it. It is possible that this is a synonym of *S. gazellae.*

***Sarcocystis woodhousei* Dogel', 1916**

Type Definitive Host. Unknown.

Type Intermediate Host. Grant's gazelle *Gazella granti.*

Location. Striated muscles of intermediate host.

Merogony. Sarcocysts compartmented, 0.25–1.5 x 0.06–0.08 mm, with thin wall with very slight radial striations. Bradyzoites in sarcocysts elongate, curved.

Remarks. Balfour (1913) said that Ross (1910) had described a sarcocyst in *G. granti* in British East Africa, but we have not seen this report. Perhaps it was this species.

See the Remarks under *Sarcocystis* spp. from *G. granti.*

***Sarcocystis* spp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Grant's gazelle *Gazella granti.*

Location. Sarcocysts in striated muscles of intermediate host.

Merogony. Kaliner, Grootenhuis and Protz (1974) found macroscopic sarcocysts (macrocysts) in 27 and microscopic sarcocysts (microcysts) in 82 of 82 *G. granti* in Kenya and Tanzania. Banko (1968) found both macrocysts 4 x 0.9 mm and microcysts 1.6 x 0.06 mm in mean size. Both contained banana-shaped bradyzoites 9 x 3.5 μm.

Remarks. Janitschke, Protz and Werner (1976) fed meat from in-

fected gazelles to dogs and cats. They obtained sporocysts 13–18 x 8–12 (mean 16 x 11) μm in the dog and sporocysts 11–16 x 8–12 (mean 13 x 9) μm in the cat. They were probably dealing with 2 species, but which was which remains to be determined.

***Sarcocystis* spp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Thomson's gazelle *Gazella thomsoni.*

Location. Sarcocysts in striated muscles of intermediate host.

Merogony. The sarcocysts found by Sachs and Sachs (1968) were 5 x 2 mm; Kaliner, Grootenhuis and Protz (1974) found both macroscopic and microscopic sarcocysts. See also Kaliner et al. (1971) and Kaliner (1976).

***Sarcocystis* sp. Levchenko, 1964**

Type Definitive Host. Unknown.

Type Intermediate Host. Gazelle *Gazella subgutturosa.*

Location. Sarcocysts in striated muscles of intermediate host.

Remarks. We have not seen the paper by Levchenko (1964) on this form but are dependent on Kalyakin and Zasukhin (1975) for knowledge of its existence.

Host Genus *Saiga*

***Eimeria ismailovi* Musaev, 1970**

Synonym. Eimeria ninakohlyakimovae Yakimoff and Rastegaieff, 1930 of Svanbaev (1958) in *Saiga tatarica.*

Type Host. Saiga *Saiga tatarica.*

Oocyst Structure. Spherical or ovoid, 21–33 x 18–28 (mean 28 x 24) μm, with smooth, "double-contoured" wall 1–2 μm thick, without micropyle or residuum. Sporocysts ovoid or spherical, 7–12 x 7–11 (mean 10 x 9) μm, with residuum. Sporozoites 4–10 x 3–5 (mean 7 x 4) μm.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species from the saiga to 73 domestic lambs.

***Eimeria manafovae* Musaev, 1970**

Synonym. Eimeria elegans Yakimoff, Gousseff and Rastegaieff, 1933 of Svanbaev (1956) in *Saiga tatarica.*

Type Host. Saiga *Saiga tatarica.*

Oocyst Structure. Ellipsoidal, 29–47 x 17–26 (mean 37 x 20.5) μm, with smooth, "double-contoured" wall 1–2 μm thick, with micropyle and polar granule, without residuum. Sporocysts ellipsoidal to spherical, 11–13 x 6–11 (mean 12 x 8) μm, without Stieda body, with residuum. Sporozoites 7–8 x 5–6 (mean 7 x 5) μm.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species from the saiga to 26 domestic lambs, 5 *O. ammon,* 2 *Capra sibirica* or 7 *Capreolus capreolus.*

***Eimeria saiga* Svanbaev, 1958**

(Fig. 208, Levine and Ivens, 1970)

Type Host. Saiga *Saiga tatarica.*

Oocyst Structure. Spherical, rarely short ovoid, 28–34 x 27–32 (mean 30.5 x 29.5) μm, with smooth, yellowish green or yellowish brown, double-contoured wall about 1 μm thick, without micropyle, with residuum, usually with polar granule. Sporocysts spherical or short ovoid, 7–12 x 7–9 (mean 10 x 8) μm, with residuum. Sporozoites spherical to ovoid, 4–6 x 3–5 (mean 5 x 4) μm.

***Eimeria sajanica* Machul'skii, 1947**

Type Host. Saiga *Saiga tatarica.*

Oocyst Structure. Because Machul'skii's (1947) paper is not available to us, we are using the information given by Svanbaev (1958). Oocysts ovoid or spherical, 18–23 x 16–20 (mean 21 x 18) μm, colorless, with double-contoured wall up to 1 μm thick, without residuum or polar granule. Sporocysts ovoid, 5–10 x 3–5 μm, with residuum.

***Eimeria tatarica* Musaev, 1970**

Synonym. Eimeria faurei (Moussu and Marotel, 1902) Martin, 1909 of Svanbaev (1958) in *Saiga tatarica.*

Type Host. Saiga *Saiga tatarica.*

Oocyst Structure. Ovoid, 25–35 x 19–30 (mean 30 x 24) μm, with smooth, "double-contoured," yellow-brown wall 1–2 μm thick, with micropyle, rarely with micropylar cap. Sporocysts ovoid, 9–13 x 6–8 (mean 10 x 7.5) μm, with residuum. Sporozoites 7–10 x 3–4 (mean 8 x 4) μm.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species from the saiga to 6 lambs.

***Eimeria tekenovi* Svanbaev, 1979**

Synonym. Eimeria arloingi (Marotel, 1905) Martin, 1909 of Svanbaev (1969) in *Saiga tatarica.*

Type Host. Saiga *Saiga tatarica.*

Oocyst Structure. Ovoid or ellipsoidal, 23–33 x 18–24 (mean 29 x 22) μm, with smooth, "double-contoured," yellow-green wall 1–2 μm thick, with micropyle and micropylar cap, without residuum or polar granule. Sporocysts ellipsoidal, 9–13 x 6–9 (mean 11 x 7) μm, without Stieda body, with residuum. Sporozoites 6–8 x 2–5 (mean 7 x 4) μm.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species from the saiga to 20 lambs.

Host Genus *Oreamnos*

***Eimeria ernsti* Todd and O'Gara, 1968**

(Fig. 213, Levine and Ivens, 1970)

Synonym. Eimeria ernesti Todd and O'Gara, 1968 *(lapsus calami).*

Type Host. Rocky Mountain goat *Oreamnos americanus.*

Oocyst Structure. Ellipsoidal, sometimes with nearly flat sides, 28–37 x 19–25 (mean 33 x 23) μm, with smooth, 2-layered wall 1.8–2.3 μm thick, outer layer light brown, about ¾ of total thickness, inner layer dark brown, membrane wrinkled in micropylar area, with an inner membrane, with micropyle, with micropylar cap, mean 9 x 3 μm, without residuum, with polar granule in freshly sporulated oocysts, rare in older oocysts. Sporocysts ovoid, 14–20 x 6–9 (mean 17 x 7) μm, with Stieda body and residuum. Sporozoites located at an angle near each end of sporocyst, with a single large, clear wrinkled globule.

***Eimeria montanaensis* Todd and O'Gara, 1968**

(Fig. 214, Levine and Ivens, 1970)

Type Host. Rocky Mountain goat *Oreamnos americanus.*

Oocyst Structure. Subspherical to ellipsoidal, flattened at micropylar end, 15–23 x 13–19 (mean 19 x 15) μm, with smooth, 2-layered wall about 1.5–2 μm thick, outer layer light blue, about ⅔ of total

wall thickness, inner layer light brown, with micropyle, with small micropylar cap on 6% of oocysts, without residuum, with polar granule. Sporocysts ovoid, 8–12 x 4–7 (mean 10 x 5) μm, with small Stieda body and residuum composed of a few fine granules between sporozoites. Sporozoites blunt, located at an angle near each end of the sporocyst, each with a large and a small clear globule.

***Eimeria oreamni* Shah and Levine, 1964**
(Fig. 216, Levine and Ivens, 1970)

Type Host. Rocky Mountain goat *Oreamnos americanus.*

Oocyst Structure. Elongate ovoid, slightly piriform, 26–34 x 17–20 (mean 29 x 19) μm, with smooth, 2-layered wall, outer layer pale greenish yellow to yellowish brown, about 1 μm thick, inner layer brownish yellow, about 0.4 μm thick, lined by a membrane usually slightly wrinkled at the micropylar end, with micropyle at the small end, without a micropylar cap or residuum, with fragmented polar granules. Sporocysts ovoid, 10–12 x 7–9 (mean 11 x 8) μm, with tiny Stieda body, with residuum usually consisting of loosely scattered granules. Sporozoites elongate, one end narrower than the other, lying lengthwise head to tail in sporocysts, with a single large clear globule at one end and sometimes one or more additional smaller clear globules in each.

***Sarcocystis* sp. Mahrt and Colwell, 1980**

Type Intermediate Host. Rocky Mountain goat *Oreamnos americanus.*

Host Genus *Rupicapra*

***Eimeria alpina* Supperer and Kutzer, 1961**
(Fig. 217, Levine and Ivens, 1970)

Type Host. Chamois Rupicapra rupicapra.

Oocyst Structure. Oocysts almost always spherical, 10–14 μm in diameter, with smooth, colorless, 1-layered, very thin wall, without micropyle, residuum or polar granule. Sporocysts subspherical, 5–6 x 4–6 μm, without residuum. Sporozoites illustrated as elongate, lying head to tail in sporocysts (Supperer and Kutzer, 1961; Kutzer, 1964; Kutzer and Hinaidy, 1969; Salzmann and Hörning, 1974).

Cross-Transmission Studies. Kutzer (1964) was unable to transmit this species to 2 sheep.

***Eimeria riedmuelleri* Yakimoff and Matschoulsky, 1940 emend. Levine and Ivens, 1970**

(Figs. 210, 211, Levine and Ivens, 1970)

Synonym. Eimeria riedmulleri Yakimoff and Matschoulsky, 1940.

Type Host. Chamois *Rupicapra rupicapra.*

Oocyst Structure. Ovoid, ellipsoidal or spherical; spherical oocysts 15–22 (mean 17.5) μm in diameter; ovoid and ellipsoidal oocysts 15–23 x 14–22 (mean 20 x 17) μm, without micropyle, residuum or polar granule. Sporocysts ovoid to spherical, 6–13 x 6–8 μm, without Stieda body or residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with a clear globule.

Cross-Transmission Studies. Restani (1968) was unable to transmit this species to a goat, a lamb or a calf.

***Eimeria rupicaprae* Galli-Valerio, 1924**

(Fig. 209, Levine and Ivens, 1970)

Type Host. Chamois *Rupicapra rupicapra.*

Oocyst Structure. Ovoid, with a flattened end, 18–33 x 13–27 μm, with or without micropyle, without residuum or polar granule, with smooth, yellowish, double-contoured wall 1 μm thick. Sporocysts presumably ovoid, 6–13 x 3–8 μm, apparently with residuum.

Cross-Transmission Studies. Restani (1968) was unable to transmit this species to a goat, a lamb or a calf.

***Eimeria suppereri* Kutzer, 1964**

(Fig. 215, Levine and Ivens, 1970)

Type Host. Chamois *Rupicapra rupicapra.*

Oocyst Structure. Ellipsoidal, generally 43–49 x 32–37 (mean 45 x 34) μm, with 2-layered wall, outer layer rough, brown, 1.5–2 μm thick, relatively difficult to separate from inner layer which is colorless to yellowish and about 1 μm thick, with micropyle in outer layer, without residuum, with 1 or 2 polar granules. Sporocysts drop-shaped, 16–19 x 9–11 μm, with residuum.

Cross-Transmission Studies. Kutzer (1964) was unable to transmit this species to 2 sheep.

***Eimeria yakimoffmatschoulskyi* Supperer and Kutzer, 1961 emend. Levine and Ivens, 1970**

(Figs 212, 273, Levine and Ivens, 1970)

Synonyms. Eimeria yakimoff-matschoulskyi Supperer and Kutzer,

1961; *E. arloingi* Marotel, 1905 of Yakimoff and Matschoulsky (1940); *E. böhmi* Supperer, 1952 of Böhm and Supperer (1956).

Type Host. Chamois *Rupicapra rupicapra.*

Oocyst Structure. Ellipsoidal or ovoid, 19–37 x 17–26 μm, with apparently 1-layered, yellowish wall 1–1.5 μm thick, with more or less distinct micropyle, with colorless micropylar cap which is easily lost, without residuum or polar granule. Sporocysts ovoid, 8–13 x 5–9 μm, with residuum.

Cross-Transmission Studies. Supperer and Kutzer (1961) were unable to transmit this species to the sheep or goat. Kutzer (1964) could not transmit it to 2 sheep. Restani (1968) said that he infected a goat and a lamb but not a calf; he apparently used no controls.

***Eimeria (?)* sp. Desser, 1978**

Desser (1978) found giant meronts containing merozoites in the bile duct epithelium of the liver of 2 chamois *Rupicapra rupicapra* on a New Zealand game farm. He thought they might be *E. riedmuelleri.*

***Sarcocystis* sp.**

Type Definitive Host. Unknown.

Type Intermediate Host. Chamois *Rupicapra rupicapra.*

Location. Sarcocysts in striated muscles of intermediate host.

Remarks. This form has been reported from Czechoslovakia by Ippen et al. (1974) and Blažek, Kotrly and Ippen (1976).

Host Genus *Ovibos*

***Eimeria faurei* (Moussu and Marotel, 1902) Martin, 1909**

Duszynski, Samuel and Gray (1977) said that they found this species in fecal samples from the muskox *Ovibos moschatus* on Bathurst Island, Canada. They did not describe it or attempt cross-transmission experiments, but said that their oocysts were 919–2,003 days old. It probably belongs to another, as yet unnamed, species.

***Eimeria granulosa* Christensen, 1938**

Duszynski, Samuel and Gray (1977) said that they found this species in fecal samples from the muskox *Ovibos moschatus* on Bathurst Island, Canada. They did not describe it or attempt cross-trans-

mission experiments, but said that their oocysts were 919–2,003 days old. It probably belongs to another, as yet unnamed, species.

***Eimeria moschati* Duszynski, Samuel and Gray, 1977**

Type Host. Musk ox *Ovibos moschatus.*

Oocyst Structure. Ellipsoidal, 17–25 x 15–20 (mean 20.5 x 17) μm, with 2-layered wall about 2 μm thick, outer layer transparent light blue, ⅔ of total thickness, inner layer dark, with micropyle, with delicate micropyle cap, without residuum, usually with polar body. Sporocysts ovoid, 9–12 x 5–7 (mean 11 x 6) μm, with Stieda body, without substiedal body, with residuum composed of small, scattered granules. Sporozoites with 1–2 clear globules.

Remarks. The oocysts were 919–2,003 days old when described from muskoxen on Bathurst Island, Canada.

***Eimeria oomingmakensis* Duszynski, Samuel and Gray, 1977**

Type Host. Muskox *Ovibos moschatus.*

Oocyst Structure. Ovoid to ellipsoidal, 38–61 x 28–38 (mean 47.5 x 34) μm, with 2-layered wall 2–4 (mean 3) μm thick, thickest on sides, outer layer bright orange, rough, about 2 μm thick, inner layer transparent, about 1 μm thick, with micropyle 6–10 μm wide in outer layer, without residuum or polar body. Sporocysts ellipsoidal, pointed at one end, 18–23 x 9–12 (mean 20 x 10.5) μm, with Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with clear globule near broad end.

Remarks. The oocysts were 919–2,003 days old when described from muskoxen on Bathurst Island, Canada.

***Eimeria ovibovis* Duszynski, Samuel and Gray, 1977**

Type Host. Muskox *Ovibos moschatus.*

Oocyst Structure. Ellipsoidal, 20–25 x 16–21 (mean 23 x 19) μm, with smooth, 2-layered wall about 1.5 μm thick, outer layer blue-gray, inner layer yellow and thinner, with micropyle in outer layer that cannot be seen in intact oocysts, with or without residuum and polar bodies. Sporocysts ellipsoidal, tapered at one end, 11–15 x 5–7 (mean 13 x 6) μm, with Stieda body, without substiedal body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with clear globule near large end.

Remarks. The oocysts were 919–2,003 days old when described from muskoxen on Bathurst Island, Canada.

***Eimeria bakuensis* Musaev, 1970**

Synonym. E. ovina Levine and Ivens, 1970.

Duszynski, Samuel and Gray (1977) said that they found this species in fecal samples from the muskox *Ovibos moschatus* on Bathurst Island, Canada. They did not describe it or attempt cross-transmission experiments, but said that their oocysts were 919–2,003 days old. It probably belongs to another, as yet unnamed, species.

***Sarcocystis* sp. Lønø, 1960**

Type Definitive Host. Unknown.

Type Intermediate Host. Muskox *Ovibos moschatus.*

Location. Sarcocysts in striated muscles of intermediate host.

Host Genus *Capra*

***Eimeria africiensis* Musaev and Mamedova, 1981**

Type Host. Domestic goat *Capra hircus.*

Location. Feces.

Oocyst Structure. Ovoid, 22–26 x 18–22 (mean 25 x 20) μm, with a smooth, 1-layered wall 1.2–1.5 μm thick, with micropyle and micropylar cap, without residuum or polar granule. Sporocysts elongate ovoid (almost ellipsoidal), 12–18 x 8–10 (mean 18 [*sic*] x 9) μm, without Stieda body, with residuum. Sporozoites elongate, with clear globule at the large end, lying lengthwise head to tail in sporocysts.

Remarks. Musaev and Mamedova (1981) said that this species is structurally identical with *E. crandallis* of the sheep. However, its sporocysts are larger.

***Eimeria ahsata* Honess, 1942**

Type Host. Rocky Mountain bighorn sheep *Ovis canadensis.*

Other Hosts. Various species of *Ovis* (see below).

Remarks. Although *E. ahsata* has been reported from *Capra* by several workers, these reports were probably of *E. christenseni.*

***Eimeria alijevi* Musaev, 1970**

(Figs. 240, 241, Levine and Ivens, 1970)

Synonyms. E. galouzoi Yakimoff and Rastegaieff, 1930 in part; *E.*

kandilovi Musaev, 1970; *E. parva* Kotlán, Mócsy and Vajda, 1929 of *auctores* in *Capra.*

Type Host. Domestic goat *Capra hircus.*

Other Hosts. Ibex *C. ibex, C. sibirica* (see Couturier, 1962).

Location. Meronts in small intestine; gamonts and oocysts in posterior small intestine, cecum and colon.

Oocyst Structure. Ellipsoidal, subspherical, spherical or ovoid, slightly narrow at micropyle end, 15–23 x 12–22 (mean 16–20 x 13–19) μm, with smooth, 2-layered wall, outer layer 0.6–0.8 (mean 0.7) μm thick, pale yellowish to colorless, inner layer 0.3–0.5 (mean 0.4) μm thick, dark brown to yellowish brown, or a dark, thin membrane, with usually inconspicuous micropyle, without micropylar cap, ordinarily with 1 polar granule that is sometimes shattered, without residuum. Sporocysts elongate to broadly ovoid, 7–13 x 4–9 (mean 9–10 x 5–7) μm, with or without Stieda body, without substiedal body, with residuum composed of a few scattered or aggregated fine granules. Sporozoites elongate, lying more or less at an angle or lengthwise, head to tail, in sporocysts, usually with 1 or 2 clear globules.

Merogony. In 4 kids that died 11–15 days after inoculation, Sayin (1966) found meronts in the epithelial cells of the villi of the middle part of the small intestine. They were up to 260 x 180 μm and could be easily seen with the naked eye as whitish bodies. He also saw much smaller meronts 15–18 x 9–12 μm in the epithelial cells of the crypts of Lieberkuehn of the small intestine in 1 kid that died.

Gamogony. In 4 kids that died 11–15 days after inoculation, Sayin (1966) found gamonts and oocysts in mucosal scrapings from the colon, cecum and posterior small intestine. They were in the epithelial cells of the mucosa. The macrogametes were 14–18 x 9–14 μm and the microgamonts 22–25 x 15–20 μm.

Prepatent Period. Seven to 12 days (Sayin, 1966; Lima, 1980).

Patent Period. Six to 18 days (Lima, 1980; Sayin 1966). Oocysts may be passed intermittently for another week or more.

Pathogenicity. According to Sayin (1966), *E. "parva"* may be markedly pathogenic for the goat. Nine of 12 Angora goats 6–10 weeks old given 25,000 to 1 million oocysts developed diarrhea, and 4 of them died 11–15 days after inoculation. Four of the survivors were challenged 6 weeks after inoculation with 5 or 10 million oocysts; none had clinical signs, and all discharged markedly fewer oocysts than after the original infection.

Cross-Transmission Studies. Tsygankov, Paichuk and Balbaeva (1963) were unable to transmit this organism (which they called *E. galouzoi)* from the goat to 1 saiga and 1 lamb, although they produced a patent infection with it in a kid. Lima (1980) could not transmit it from the goat to lambs. Svanbaev (1979) failed to transmit it from the goat to 25 lambs.

Remarks. No cross-transmission attempts have apparently been made between *C. hircus* and *C. sibirica.* Unless they have been made and have failed, *E. kandilovi* must be considered a synonym of *E. alijevi.*

***Eimeria absheronae* Musaev, 1970 emend. Musaev and Mamedova, 1981**

(Fig. 232, Levine and Ivens, 1970)

Synonyms. Eimeria faurei (Moussu and Marotel, 1902) Martin, 1909 of *auctores* from *Capra hircus; Eimeria aemula* Yakimoff, 1931 in the goat; *Eimeria apsheronica* Musaev, 1970.

Type Host. Domestic goat *Capra hircus.*

Other Hosts. Ibex *Capra ibex* and probably Siberian mountain goat *C. sibirica.*

Location. Small intestine.

Oocyst Structure. Ovoid, slightly flattened at narrower, micropylar end, 24–37 x 18–26 (mean 29–31 x 22–23) μm, with 1–2-layered, smooth, faint green to greenish yellow-brown wall, outer layer about 0.3–0.5 μm thick, colorless, inner layer about 0.8–1.2 μm thick, pale, transparent yellowish or slightly pinkish, with micropyle with or without a small internal plug, without micropylar cap, with polar granule (usually shattered), without residuum. Sporocysts piriform or ellipsoidal, with one end often pointed, 11–17 x 7–11 μm, with or without Stieda body, without substiedal body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, usually with 1 or 2 large clear globules.

Prepatent Period. 14–17 days (Lima, 1980).

Patent Period. 4–9 days (Lima, 1980).

Cross-Transmission Studies. Krylov (1961) was unable to transmit this species from the goat to the sheep, or *E. faurei* from the sheep to the goat. Tsygankov, Paichuk and Balbaeva (1963) were unable to transmit *E. absheronae* (which they called *E. aemula)* from the goat to 1 lamb and 1 saiga. In an uncontrolled experiment, Subramanian and

Jha (1966) said that they transmitted "*E. faurei*" from the goat to a lamb by feeding it 160,000 sporulated oocysts. Lima (1980) failed to transmit this species from the goat to the sheep. Svanbaev (1979) failed to transmit it from the goat to 25 lambs.

***Eimeria arloingi* (Marotel, 1905) Martin, 1909**
(Figs. 218–225, Levine and Ivens, 1970)

Synonyms. Coccidium arloingi Marotel, 1905; *C. caprae* Jaeger, 1921; *Eimeria ahsata* Honess, 1942 of Chevalier (1966) from the goat; [*non*] *E. ahsata* Honess, 1942 of Chevalier (1965) from the sheep; *E. crandallis* Honess, 1942 of Chevalier (1966) from the goat; *E. faurei* (Moussu and Marotel, 1902) of Tsygankov, Paichuk and Balbaeva (1963) and of some other Russian authors; *E. hawkinsi* Ray, 1952 in part (reports from the goat).

Type Host. Domestic goat *Capra hircus.*

Location. Small intestine. Lima (1979), among others, found meronts and oocysts, presumably of this species, in the mesenteric lymph nodes.

Oocyst Structure. Ellipsoidal or slightly ovoid, slightly flattened at the micropylar end, 22–36 x 16–26 (mean 28 x 19–21) μm, with 2-layered wall, outer layer smooth, colorless, 1 μm thick, inner layer brownish yellow, 0.4–0.5 μm thick, inner layer forming a membrane which is often slightly wrinkled at the micropylar end, with micropyle at small end of oocyst, ordinarily with prominent, colorless, mound-shaped micropylar cap, mean 2 x 6–7 μm, ordinarily with 1 or more polar granules which sometimes appear to be shattered into many rather fine particles, without residuum. Sporocysts elongate ovoid, with a rather truncate small end, 10–17 x 5–10 μm, without Stieda body or with a vestigial one, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, usually with a large clear globule at the large end and a small one at the small end.

Merogony. There are 2 generations of meront. The first-generation meronts are in the endothelial cells of the lacteals of the villi, in Peyer's patches in the duodenum, jejunum and ileum, and also in the sinuses of the mesenteric lymph nodes draining these regions. They are giant meronts, 139–359 x 68–243 (mean 247 x 147) μm and contain many thousands of merozoites 9–12 x 1–2 (mean 10 x 1.4) μm. Immature meronts are seen 6 days after inoculation, and mature ones 9–20 days after inoculation. Second-generation meronts

are in the epithelial cells of the villi and crypts of the small intestine. Mature ones are first seen 12 days after inoculation. They are 11–44 x 9–20 (mean 22 x 12) μm and contain 8–24 merozoites 4–10 (mean 7.5) μm long. A residuum is sometimes present (Sayin, Dincer and Milli, 1980).

Gamogony. Numerous diffusely scattered, pale yellow to white focal plaques about 0.5 cm in diameter are in the mucosa of the duodenum, jejunum and ileum; a few are present in the first third of the colon. The plaques consist essentially of masses of macrogametes, microgamonts and young oocysts in the epithelial cells of the tips and sides of the villi and also in the crypts. The mature macrogametes are 12–28 x 8–20 μm. The mature microgamonts are 11–34 x 8–29 μm and contain several hundred crescentic or comma-shaped microgametes about 3.5 μm long and 0.4 μm wide (Levine, Ivens and Fritz, 1967; Sayin, 1965; Sayin, Dincer and Milli, 1980).

Prepatent Period. 14–17 days (Sayin, Dincer and Milli, 1980).

Patent Period. 14–15 days (Sayin, Dincer and Milli, 1980).

Pathogenicity. This species is pathogenic for the goat, causing hyperplasia of the small intestine with pseudo-adenomatous metaplasia of the villi, atrophy of the crypts of Lieberkuehn and cellular infiltration of the mucosa in kids. There are white to pale yellow plaques 0.3–0.4 mm in diameter, with irregular edges, in the small intestine.

Artificially inoculated kids have severe diarrhea and most die from coccidiosis during the patent or prepatent period. They have marked intestinal inflammation, edema, epithelial necrosis, leukocyte infiltration, hyperplasia and diffusely scattered yellow plaques in the mucosa of the small intestine (Levine, Ivens and Fritz, 1962; Deiana and Delitala, 1953; Gill and Katiyar, 1961; Sharma Deorani, 1966; Sayin, 1965).

Cross-Transmission Studies. Krylov (1961), Svanbaev (1963, 1979), Sayin, Dincer and Milli (1980), and Lima (1980) were unable to infect the sheep with this species.

Remarks. Unless it is proven otherwise, we feel that coccidia reported as *E. arloingi* by various authors from ruminants other than the goat do not actually belong to this species. These hosts include *Ovis aries, O. canadensis, O. ammon, O. musimon, Hemitragus jemlahicus, Rupicapra rupicapra, Cervus elaphus, Dama dama, Capreolus capreolus and Gazella subgutturosa.*

***Eimeria babaevi* Svanbaev, 1979**

Synonym. Eimeria ninakohlyakimovae Yakimoff and Rastegaieff, 1930 of Svanbaev (1958) in *Capra sibirica.*

Type Host. Siberian mountain goat *Capra sibirica.*

Oocyst Structure. Ovoid or spherical, 21–25 x 19–24 (mean 23 x 21) μm, with smooth, yellow-green, yellow-brown or orange-brown, "double-contoured" wall 1.2–1.6 μm thick, without micropyle or residuum. Sporocysts spherical or ovoid, 7–12 x 6–8 (mean 10 x 7) μm, with residuum. Sporozoites 3–7 x 2–4 (mean 5 x 3) μm.

Cross-Transmission Studies. Svanbaev (1979) failed to transmit this species from *C. sibirica* to 18 lambs, 5 saigas, 5 *Ovis ammon* or 13 *Capreolus capreolus,* although he transmitted it to a *C. sibirica* kid. No attempts have apparently been made at cross-transmission between *C. sibirica* and *C. hircus.*

Remarks. The above description is based on Svanbaev (1979). He did not give an illustration. This name is probably a synonym of *E. ninakohlyakimovae,* but we are retaining it separately for the present.

***Eimeria capra* Musaev, 1970**

Synonym. Eimeria faurei (Moussu and Marotel, 1902) Martin, 1909 of Svanbaev (1958) in *Capra sibirica.*

Type Host. Siberian mountain goat *Capra sibirica.*

Oocyst Structure. Ovoid, 23–32 x 20–26 (mean 27 x 22) μm, with yellow, yellow-green, yellow-brown or orange-brown wall, with micropyle and micropylar cap, without residuum. Sporocysts ovoid, 8–13 x 7–9 (mean 10 x 8) μm, with residuum. Sporozoites 3–7 x 2–4 (mean 5 x 2) μm.

Cross-Transmission Studies. Svanbaev (1979) failed to transmit this species from *C. sibirica* to 16 lambs, 2 *Saiga tatarica,* or 1 *Capreolus capreolus.*

***Eimeria caprina* Lima, 1979** (Fig. 323)

Type Host. Domestic goat *Capra hircus.*

Oocyst Structure. Ellipsoidal or slightly ovoid, slightly flattened at micropylar end, 27–40 x 19–26 (mean 32 x 23) μm, with smooth, 2-layered wall, outer layer about 1.1 μm thick, dark brown to brownish yellow, inner layer about 0.6 μm thick, colorless, with micropyle 5–7 μm in diameter, without micropylar cap, ordinarily with 1 or more

polar granules that are sometimes shattered, without residuum. Sporocysts ovoid, 13–17 x 7–10 (mean 15 x 8.5) μm, with small Stieda body, without substiedal body, with residuum of many scattered granules. Sporozoites elongate, lying lengthwise head to tail in sporocysts, usually with large clear globule at large end and a smaller one at the small end.

Prepatent Period. 17–20 days.

Patent Period. 3–6 days.

Cross-Transmission Studies. Lima (1979) was unable to transmit this species from the goat to the sheep.

***Eimeria caprovina* Lima, 1980**(Fig. 322)

Type Host. Domestic goat *Capra hircus.*

Other Host. Domestic sheep *Ovis aries* (experimental).

Oocyst Structure. Ellipsoidal, subspherical or slightly ovoid, usually flattened at micropyle end, 26–36 x 21–28 (mean 30 x 24) μm, with smooth, 2-layered wall, outer layer about 1 μm thick, colorless, inner layer about 0.6 μm thick, dark brown to brownish yellow, with micropyle 4–10 (mean 6) μm in diameter, without micropyle cap, with 1–4 or many polar granules, without residuum. Sporocysts elongate ovoid, 13–17 x 8–9 (mean 14 x 8) μm, with Stieda body, without substiedal body, with residuum composed of many scattered granules. Sporozoites elongate, lying lengthwise head to tail in sporocysts, usually with 2 large clear globules, 1 at each end.

Prepatent Period. 14–20 days.

Patent Period. 4–9 days.

Cross-Transmission Studies. Lima (1980) transmitted this species from the goat to sheep and back to goats.

***Eimeria christenseni* Levine, Ivens and Fritz, 1962**
(Fig. 234, Levine and Ivens, 1970)

Synonym. Eimeria tirupatiensis Sivanarayana and Venkataratnam, 1969; *E. ahsata* in goats (?); *E. tuniensis* Musaev and Mamedova, 1981.

Type Host. Domestic goat *Capra hircus.*

Location. Small intestine and presumably mesenteric lymph nodes (Lima, 1979).

Oocyst Structure. Ovoid, sometimes ellipsoidal, slightly flattened at micropylar end, 27–44 x 17–31 μm, with 2-layered wall, outer layer

smooth, colorless to very pale yellowish, 0.8–1.2 μm thick, inner layer brownish yellow, 0.4–0.7 μm thick; inner layer forms a membrane which is usually wrinkled at the micropylar end; with micropyle at small end of oocyst, with prominent, colorless, mound-shaped micropylar cap, with 1 or more polar granules, sometimes partly shattered into many rather fine particles, without residuum. Sporocysts ovoid, 12–18 x 8–11 (mean 15–16 x 9–10) μm, without Stieda body or with vestigial one, without substiedal body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts with large, clear globule at one end and sometimes 1 or more additional smaller, clear globules at the other end.

Merogony. Lima (1980a, 1981) found giant first-generation meronts in the endothelial cells of the lacteals of the jejunum, ileum, lamina propria, submucosal lymph vessels and mesenteric lymph nodes in kids beginning 6 days after inoculation. In the mesenteric lymph nodes they were in cells of the sinuses, trabeculae, medulla, hilus, lymph vessels of the hilus and pericapsular connective tissue. They grew until, when mature at 14 days, they were ellipsoidal, 100–277 x 81–130 (mean 184 x 100) μm, and contained thousands of straight merozoites about 6–8 x 1–2 μm. He saw second-generation meronts 16 days after inoculation, mostly in epithelial cells of the crypts and less frequently in those of the villi in the small intestine and in the sinuses of the mesenteric lymph nodes. They were 9–20 x 8–12 (mean 14 x 10) μm and contained 8–24 merozoites which lay parallel to each other like a bundle of sticks. He sometimes saw a residuum.

Gamogony. Lima (1980) first saw gamonts 16 days after inoculation. They were in epithelial cells of the small intestine, mostly 4–6 m from the abomasum. The mature macrogametes were 19–35 x 13–25 (mean 26 x 19) μm. The mature microgamonts were 19–50 x 12–40 (mean 34 x 26) μm and contained hundreds of microgametes which lay in whorls on their surface; a residuum was present. The microgametes were crescent- or comma-shaped, about 3 x 0.5 μm. The macrogametes, microgamonts and intracellular oocysts occurred in large groups which formed macroscopic white areas in the intestinal mucosa.

Prepatent Period. 14–23 days (Lima, 1980a, 1981).

Patent Period. Eight to more than 30 days (Lima, 1980a, 1981).

Pathogenicity. This species is one of the most pathogenic coccidia of goats. Lima (1980) saw no gross changes in kids killed 2–3 days after experimental inoculation, but he found congested areas in the lower jejunum and ileum of kids killed 4–8 days after inoculation, hemorrhages in the small intestine of a kid that died 20 days after inoculation and in kids killed 14–26 days after inoculation, and numerous pale yellow to white foci in the small intestine 4–8 m from the abomasum of the kid killed 26 days after inoculation during the peak of oocyst production. At 20–26 days the intestinal contents were liquid, yellowish brown and contained pieces of mucosa. The mesenteric lymph nodes are enlarged 4–26 days after inoculation.

The predominant histopathologic lesions are in the small intestine. There are numerous giant meronts in the lacteals and less frequently in the lamina propria among the crypts and inside lymphatic vessels in the submucosa. Focal infiltration with lymphocytes and plasma cells, epithelial necrosis and submucosal edema are usually associated with focal aggregates of coccidia, especially gamonts and oocysts, in the jejunum and ileum. Superficial desquamation of the mucosa and superficial necrosis occur. The capillaries are congested and petechial hemorrhages are present. The cellular reaction in the lamina propria and submucosa consists of lymphocytes, macrophages, plasma cells, polymorphonuclear leukocytes and eosinophils. Edema and pericapsular infiltration by lymphocytes occurs in the mesenteric lymph nodes.

The white foci in the intestine consist essentially of masses of microgamonts, macrogametes and oocysts in the epithelial cells of the tips and sides of the villi and in the crypts.

Cross-Transmission Studies. McDougald (1979) and Lima (1980) could not transmit this species from the goat to the sheep.

Remarks. Various reports of *E. ahsata* in goats were more likely of *E. christenseni.*

***Eimeria crandallis* Honess, 1942**

Type Host. Rocky Mountain bighorn sheep *Ovis canadensis.*

Remarks. This species has been reported from domestic and wild goats in addition to several species of sheep and deer. It is doubtful if it actually occurs in any host genus other than *Ovis.* Reports of this species in goats probably have been of *E. hirci* or perhaps *E. africiensis.* Information regarding *E. crandallis* is given below under *Ovis.*

***Eimeria gilruthi* (Chatton, 1910) Reichenow and Carini, 1937**

For a discussion of this species, see the entry under *Ovis*. Actually, we believe that the organisms that have been called *E. gilruthi* in the sheep and goat are actually giant meronts of other species, but we do not know what it or they are.

***Eimeria hirci* Chevalier, 1966**

(Fig. 265, Levine and Ivens, 1970)

Synonym. Eimeria crandallis Honess, 1942 of *auctores* from goat.

Type Host. Domestic goat *Capra hircus.*

Other Hosts. Capra sibirica, C. aegagrus, C. ibex.

Oocyst Structure. Ellipsoidal to spherical, slightly flattened at micropyle end, 17–29 x 14–22 (mean 21–23 x 16–19) μm, with smooth, 1–2-layered wall, outer layer 0.7–1.0 (mean 0.8) μm thick, colorless, inner layer 0.4–0.6 (mean 0.5) μm thick, light brown to brownish yellow, lined by a membrane which is slightly wrinkled at the micropylar end, with micropyle (sometimes imperceptible), with or without colorless, mound-shaped or slightly pointed micropylar cap, with 1 or more polar granules, without residuum. Sporocysts usually broadly ovoid, 8–13 x 5–9 (mean 10–11 x 6.5–7) μm, with tiny Stieda body (ordinarily not seen), without substiedal body, ordinarily with residuum composed of few-to-many usually scattered granules. Sporozoites lie lengthwise, or at more or less of an angle or even at ends of sporocysts, with 1 or 2 clear globules.

Prepatent Period. 13–16 days (Lima, 1980).

Patent Period. 6–14 days (Lima, 1980).

Cross-Transmission Studies. Lima (1980) could not infect the sheep with *E. hirci* from the goat.

***Eimeria ibicis* Colombo, 1958**

Synonyms. ?Eimeria faurei of *auctores* in *Capra ibex; ?Eimeria caprae* Jaeger, 1921 (according to Pellérdy, 1963).

Type Host. Ibex *Capra ibex.*

Oocyst Structure. Ovoid, bright rose, apparently smooth, 27 x 18 μm, with micropyle, without micropylar cap or residuum. No other information given.

Remarks. Whether this is a valid species remains to be determined.

***Eimeria jolchijevi* Musaev, 1970**

Synonym. Eimeria granulosa Christensen, 1938 of *auctores* from *Capra.*

Type Host. Domestic goat *Capra hircus.*

Oocyst Structure. Ellipsoidal or ovoid, slightly broader at micropyle end, which is slightly flattened, 26–37 x 18–26 (mean 31–32 x 22–23) μm, with smooth, 2-layered wall, outer layer 0.9–1.2 (mean 1.0) μm thick, pale yellow to yellowish brown or colorless, inner layer 0.5–0.8 (mean 0.6) μm thick, dark brown to brownish yellow, with micropyle at broad end, with prominent light brown to pale yellow, mound-, cone- or shallow bowl-shaped, easily dislodged micropylar cap, with 1 or more (sometimes shattered) polar granules, without residuum. Sporocysts elongate ovoid, usually rounded at both ends, 12–18 x 6–10 (mean 15 x 8) μm, with small Stieda body, without substiedal body, with residuum composed of many scattered granules. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 1–2 or more large clear globules.

Prepatent Period. 14–17 days (Lima, 1980).

Patent Period. 3–10 days (Lima, 1980).

Cross-Transmission Studies. Lima (1980) could not infect the sheep with *E. jolchijevi* from the goat. Musaev (1970) said that many authors had been unable to transmit this species from the goat to the sheep.

***Eimeria kocharii* Musaev, 1970**

Synonyms. Eimeria intricata Spiegl, 1925 of *auctores* in *Capra; Eimeria nazijrovi* Svanbaev, 1979.

Type Host. Domestic goat *Capra hircus.*

Other Hosts. Ibex *Capra ibex,* Siberian mountain goat *C. sibirica.*

Oocyst Structure. Ellipsoidal or slightly ovoid, 39–59 x 27–47 μm, with 2-layered wall, outer layer irregular, granular, brownish yellow to dark brown, 2–3 μm thick, transversely striated and appearing divided into 2 sublayers by a faint line, inner layer dark brown, 0.4–0.8 μm thick, lined by a membrane which is often wrinkled at micropylar end, with micropyle in outer layer only, with prominent, dome-shaped, colorless to greenish yellow, detachable micropylar cap, with 1 or more polar granules, without residuum. Sporocysts elongate ovoid, with one end bluntly pointed, 17–22 x 9–14 (mean 20 x 11–14) μm, without Stieda body or with an extremely tiny one, with residuum. Sporozoites elongate, with one end narrower than the other, lying lengthwise head to tail in sporocysts, with 2–3 clear globules.

Cross-Transmission Studies. Svanbaev (1979) failed to transmit *E. kocharii* from the domestic goat to 25 lambs.

Remarks. Apparently no cross-transmission attempts have been made between domestic goats and *Capra sibirica* or *C. ibex.* In their absence, we are synonymizing *E. nazijrovi* (which Svanbaev [1979] named from the Siberian mountain goat *Capra sibirica)* with *E. kocharii.*

Eimeria nana Yakimoff, 1933

Type Host. Siberian mountain goat *Capra sibirica.*

Oocyst Structure. Spherical (98%) or ovoid (2%); spherical oocysts 15–18 (mean 16) μm in diameter, ovoid ones 16.5–18 x 15–16.5 μm; oocysts dull, with double-contoured wall, without residuum. Sporocysts 6 x 4.5 μm, with residuum. No other information given.

Remarks. It is uncertain whether this is a valid species. Further research is needed on the coccidia of *C. sibirica* before the matter can be resolved.

Eimeria ninakohlyakimovae Yakimoff and Rastegaieff, 1930 emend. Levine, 1961

(Figs. 226, 228, Levine and Ivens, 1970)

Synonyms. Eimeria nina-kohl-yakimovi Yakimoff and Rastegaieff, 1930; *E. galouzoi* Yakimoff and Rastegaieff, 1930 in part.

Type Host. Domestic goat *Capra hircus.*

Other Hosts. Wild goat *Capra aegagrus,* ibex *C. ibex.* In addition, this species has been reported from *Gazella subgutturosa, Capreolus capreolus, Cervus elaphus, Dama dama,* and *Rupicapra rupicapra.* It has also been reported many times from *Ovis,* but these reports were actually of *E. ovinoidalis* (see below).

Location. Small intestine, especially the posterior part, and also cecum and colon.

Oocyst Structure. Ellipsoidal or subspherical to slightly ovoid, usually slightly flattened at micropyle end, 19–28 x 14–23 (mean 24 x 19) μm, with smooth, 2-layered wall, outer layer 0.7–1.0 (mean 0.8) μm thick, slightly yellowish or colorless, inner layer 0.4–0.6 (mean 0.5) μm thick, dark brown to yellowish brown, usually with micropyle at narrow end, without micropylar cap, with 1 or more polar granules, sometimes shattered, without residuum. Sporocysts elongate ovoid, 9–15 x 4–10 (mean 12 x 6.5) μm, with Stieda body at narrow end, without substiedal body, with residuum of many scattered gran-

ules. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 1 large and 1 small clear globule.

Merogony. The meronts are 15–35 μm in diameter and contain 40–200 merozoites 1.5–2 μm in diameter. They are in the epithelial cells of the glands of Lieberkuehn in the duodenum 3–4.5 m from its anterior end (Balozet, 1932b,c).

Sayin (1964) found 1 type of meront in Angora goats. They were ellipsoidal or spherical, 31–43 x 22–31 (mean 37 x 26.5) μm, and were in the epithelial cells of the ileum, cecum and upper part of the large intestine.

Gamogony. Balozet (1932b, c) said that the microgamonts are 45–50 μm in diameter; they are apparently in the epithelial cells of the glands of Lieberkuehn in the duodenum 3–4.5 m from its anterior end. The microgametes are 3–4 μm long and have a flagellum 1–2 μm long. The macrogametes are apparently in the same type of host cell.

Sayin (1964) said that gamonts and oocysts are present in the epithelial cells of the ileum, cecum and upper part of the large intestine. The microgamonts are 20–25 x 15–18 (mean 22.5 x 16.5) μm, and have whorls of microgametes on their surface and some residual material in the center. The mature macrogametes are 9–18 x 7–13 (mean 13.5 x 10) μm.

Prepatent Period. 10–13 days (Balozet, 1932b, c).

Pathogenicity. This species may cause mucous or mucosanguinous diarrhea followed by death (Balozet, 1932a). Sayin (1964) found numerous round, smooth white plaques about 0.2–0.3 mm in diameter in the mucosae of the small intestine, cecum and colon. There was slight to moderate enteritis. The cellular reaction consisted of lymphocytes and polymorphonuclear leukocytes.

Cross-Transmission Studies. This species cannot be transmitted to sheep (Balozet, 1932a; Lotze et al., 1961; Tsygankov, Paichuk and Balbaeva, 1963; Svanbaev, 1979).

***Eimeria pallida* Christensen, 1938**

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Domestic goat *Capra hircus,* ibex *C. ibex* (see Couturier, 1962). The following discussion refers only to the goat. See under *Ovis* for a discussion of this species in sheep.

Oocyst Structure. Ellipsoidal or slightly ovoid, 13–18 x 10–14

(mean 16 x 12) μm, with a smooth, colorless to very pale yellow, 2-layered wall, outer layer 0.6 μm thick, inner layer merely a dark line on the inner surface of the wall, with imperceptible micropyle, without micropylar cap or residuum, with polar granule. Sporocysts ovoid, 6–9 x 4–5 (mean 7 x 5) μm, without Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with a single clear globule.

Remarks. It is likely that this name actually refers to different species in the sheep and goat.

***Eimeria punctata* Landers, 1955**

(Fig. 253, Levine and Ivens, 1970)

Synonym. Eimeria honessi Landers, 1952; [*non*] *E. honessi* Alderson, 1951 *nomen nudum;* [*non*] *E. media* var. *honessi* Carvalho, 1943.

Type Host. Domestic sheep *Ovis aries.*

Other Host. Domestic goat *Capra hircus* (Chevalier, 1966). The following discussion refers only to *Capra.* See under *Ovis* for a discussion of this species in sheep.

Oocyst Structure. Ovoid to ellipsoidal, 21–31 x 15–23 (mean 26 x 19.5) μm, with a broad micropyle and a high, transparent micropylar cap, and a greenish yellow to brownish green wall composed of several layers and pitted like a thimble. Sporocysts slender.

Remarks. Further study is needed to determine whether the forms in the sheep and goat actually belong to the same species.

***Eimeria skrjabini* Dashnyam, 1961**

This species was described from the goat in the Mongolian People's Republic in the proceedings of the Seventh Conference on Infectious Diseases of Livestock in Moscow. We have not seen the report; it was referred to by Svanbaev (1977) without any description.

***Cryptosporidium muris* Tyzzer, 1907**

Mason, Hartley and Tilt (1981) found *Cryptosporidium muris* sp. in the brush border of the small intestine enterocytes of a kid goat in Australia that had diarrhea and died.

***Sarcocystis capracanis* Fischer, 1979**

Type Definitive Host. Domestic dog *Canis familiaris.*

Other Definitive Host. Coyote *Canis latrans.*

Type Intermediate Host. Domestic goat *Capra hircus.*

Location. Striated muscles, brain and blood vessel endothelia of goat; small intestine of dog.

Oocyst Structure. Oocysts not described. Sporocysts 12–15 x 9–10 (mean 14 x 9.5) μm.

Merogony. Fischer (1979), Aryeetey, Mehlhorn and Heydorn (1980) and Heydorn and Haralambidis (1982) studied the life cycle, the latter two using the dwarf goat *Capra aegagrus hircus.* There are 2 pre-muscle meront generations, mainly in the endothelial cells of all organs, including the brain. On day 20 they are especially common in the glomeruli of the kidneys. First-generation meronts can be found 10–12 days after inoculation. They are up to 30 x 12 μm, have a 3-layered pellicle and contain at least 46 merozoites 6–8 x 2–4 μm. Second-generation meronts can be found in the same locations 20–23 days after inoculation. They are structurally identical with the first-generation meronts.

Sarcocysts can be found in the cells of the tongue, heart, diaphragm, skeletal muscles and brain 43 days after inoculation. At first they contain only metrocytes, but bradyzoites appear about day 65; metrocytes can be found even later, however. The bradyzoites are banana-shaped, about 12–16 x 3–5 μm, have a 3-layered pellicle, and contain rhoptries, micronemes, conoid, 22 subpellicular microtubules, polysaccharide granules, etc. The sarcocysts are 130–800 x 50–70 μm on day 92, but may be up to 3 mm long in naturally infected goats. They are septate and have a striated wall about 2.8 μm thick. By day 92 they bear protrusions 2.5–3.5 μm long and 1.2 μm in diameter.

Gamogony. This occurs in the duodenum and jejunum of the dog. Syngamy occurs 13–24 hours after inoculation. The sporocysts are 13–15 x 9–10 μm.

Prepatent Period. 7–8 days.

Patent Period. Several weeks.

Pathogenicity. This species is usually not pathogenic for the dog, but may cause a watery diarrhea for about a day after dogs have been fed heavily infected goat muscle tissue (Heydorn and Haralambidis, 1982).

Fischer (1979) found that the first- and second-generation meronts were pathogenic for the goat. Inoculation with 50,000 to 2 million sporocysts by mouth caused all goats to become ill within 20 days.

Characteristic clinical signs included very high body temperature and anemia. Two goats fed 2 million sporocysts each and 1 goat each of those fed 100,000, 80,000, and 50,000 sporocysts, respectively, died 20–65 days after inoculation. Two goats fed 80,000 and 100,000 sporocysts, respectively, were killed on days 31 and 43 while moribund.

Dubey et al. (1981) found that 10–40 million sporocysts killed goats in 11–13 days with interstitial pneumonia, vasculitis and necrosis of the mesenteric lymph nodes; 100,000 or 1 million sporocysts caused death in 19–23 days with clinical signs of anorexia, fever, anemia and weight loss; 50,000 sporocysts killed 4 goats in 24–68 days; 10,000 sporocysts killed 1 of 4 goats in 61 days; and 1,000 sporocysts had no clinical effect. Alanine aminotransferase, lactic dehydrogenase, blood urea nitrogen and bilirubin were increased, and they found thymic atrophy, vasculitis, hepatitis, cholangitis, myocarditis, generalized myositis and encephalomyelitis on histologic examination. The signs were due to the first 2 generations of meronts. If the animals survived the first 5 weeks of infection, they generally recovered. Dubey (1981b,e) found that 10,000 or 1 million sporocysts caused abortion or death; some goats were killed by feeding as few as 10,000 sporocysts; 1,000 sporocysts had no apparent effect. He (1982a) said that the LD_{50} in goats is 10,000 sporocysts.

Collins, Sutton and Charleston (1980) found that 5 million sporocysts caused illness in goats beginning on day 18. The temperature rose progressively, peaking at days 6, 11 and 18. At 18–19 days, they saw multiple petechiation and merogony in the endothelial cells. Smaller numbers of sporocysts caused lowered hemoglobin, packed cell volume and total protein levels beginning on day 17.

Dubey (1983) found that a subclinical dose of *S. capracanis* sporocysts could kill the feti of pregnant goats although the goats themselves showed no clinical signs. Abortion in challenged does occurred before second-generation meronts developed. Pregnancy impaired *Sarcocystis*-induced immunity.

Immunity. Dubey (1981e) found that "vaccination" of goats by feeding 100–1,000 sporocysts produced immunity in some of them against subsequent feeding of 100,000 sporocysts, but that "vaccination" with 10 sporocysts did not. Collins, Sutton and Charleston (1980) found that inoculation of goats with sporocysts from the dog caused the indirect fluorescent antibody test titer to rise beginning on day 28.

Cross-Transmission Studies. Fischer (1979) could not infect 2 sheep with this species.

Cultivation. Mehlhorn, Becker and Heydorn (1978) cultivated this species in dog kidney but not in human fibroblast, cat lung or pig kidney cell cultures. Oocysts were produced and started to sporulate.

Remarks. Chhabra and Mahajan (1978) found *Sarcocystis* sp. sarcocysts in the esophageal tissues of 2 of 71 goats in India, and transmitted it to dogs.

The sporocysts resembled those of *S. tenella,* but these authors did not mention *S. moulei* or *S. orientalis* (see below).

Others who have found *Sarcocystis* sp. in goats are Sen (1951), Seneviratna, Atureliva and Vijayakumar (1975), Pethkar (1980), Pethkar and Shah (1982), all in India or Sri Lanka; and Collins and Crawford (1978) and Collins and Charleston (1979) in Australia.

Dubey (1980) transmitted what he considered to be *S. capracanis* from the goat to the coyote *Canis latrans* in Montana. Pethkar (1980) and Collins and Charleston (1979) also transmitted this form to the dog.

Pethkar and Shah (1982a) were unable to transmit this species to the sheep. The number of species of *Sarcocystis* in the goat remains to be determined.

***Sarcocystis caprifelis* El Refaii, Abdel-Baki and Selim, 1980**

Type Definitive Host. Cat *Felis catus.*

Type Intermediate Host. Goat *Capra hircus.*

Location. Striated muscles of goat.

Merogony. Pre-muscle meronts and merozoites, if any, unknown. Sarcocysts with a thin or smooth wall, "with many fibrils seen almost clear at the apex." Metrocytes and bradyzoites not mentioned.

Prepatent Period. 12 days.

Remarks. This species, if valid, must be described more completely.

***Sarcocystis moulei* Neveu-Lemaire, 1912**

Synonym. Sarcocystis orientalis Machul'skii and Miskaryan, 1958 (?).

Type Definitive Host. Unknown.

Type Intermediate Host. Domestic goat *Capra hircus.*

Location. Striated muscles of goat.

Merogony. Neveu-Lemaire (1912) said that this species has larger

sarcocysts than *S. gigantea,* and that its wall is thicker and has more apparent striations. He gave no further structural information.

Pathogenicity. According to Neveu-Lemaire (1912), this species apparently causes no special signs in the goat.

Remarks. Pethkar (1980) reported "*S. moulei*" in goats in India, but it had microscopic sarcocysts and is discussed below under *Sarcocystis* sp.

***Sarcocystis orientalis* Machul'skii and Miskaryan, 1958**

Type Definitive Host. Unknown.

Type Intermediate Host. Wild goat *Capra sibirica.*

Location. Striated muscles of intermediate host's esophagus.

Merogony. The sarcocysts in the muscles are about 3.5–7.5 x 2.5 mm, and the merozoites are elongate, with one end narrow and the other broad, 9–14 x 2–6 μm.

Remarks. This species does not appear to differ significantly from *S. moulei* of the domestic goat, and it may very well be a synonym. However, cross-transmission studies will be necessary to be sure of this.

***Sarcocystis* sp. Iyer, 1971**

Iyer (1971) found a sarcocyst 148 x 74 μm in a section of the cerebrum of a goat that had died of pneumonia and enteritis. It contained banana-shaped merozoites 10–12 x 3–4 μm and caused no cellular reaction in the brain.

***Sarcocystis* sp. Biocca, Balbo, Guarda and Costantini, 1975**

Type Definitive Host. Fox *Vulpes vulpes.*

Other Definitive Hosts. Canadian timber wolf *Canis lupus,* domestic dog *C. familiaris.*

Type Intermediate Host. Ibex (steinbok) *Capra ibex.*

Location. Feces of fox, wolf and dog; muscles of ibex.

Oocyst Structure. Oocysts not described. Sporulated sporocysts ellipsoidal, 13–15 x 8–10 μm, without Stieda body, with residuum. Sporozoites elongate.

Prepatent Period. 11 days in the fox, 12 days in the wolf, 20 days in the dog.

Patent Period. 62 days in the fox, 67 days in the wolf, 66 days in the dog.

Cross-Transmission Studies. Biocca et al. (1975) found sporocysts of this species in the feces of an unspecified number of foxes *Vulpes vulpes* and in the muscles of the ibex (steinbok) in the National Park of Gran Paradiso, Italy. They transmitted it to the fox, wolf, and dog but not to the domestic cat, lion, ferret or kestrel *Falco tinnunculus* by feeding them sarcocyst-infected esophageal, heart, diaphragm, intercostal and abdominal muscles from an infected ibex.

Sarcocystis sp. (Pethkar, 1980) nom. nov.

Synonym. Sarcocystis moulei of Pethkar, 1980, [*non*] *S. moulei* Neveu-Lemaire, 1912.

Type Definitive Host. Dog *Canis familiaris.*

Type Intermediate Host. Domestic goat *Capra hircus.*

Location. Lamina propria of anterior half of small intestine of dog. Early meronts in endothelial cells of blood vessels of visceral organs of goat; sarcocysts in striated muscles of goat.

Geographic Distribution. Asia (India).

Oocyst Structure. Neither oocyst nor sporocyst structure described.

Merogony. Pethkar (1980) studied merogony leading to sarcocyst formation in 5 kids. On days 21 and 23 he found meronts in the endothelial cells of the blood vessels of most organs. They had 2 distinct forms, indicating that there may be 2 generations. The larger ones were 40 x 30 μm and were found in the liver, heart and diaphragm. The smaller ones were 20 x 10 μm and were found in all organs examined. On day 23, there were a very few sarcocysts in the heart muscle; they were very small and had an indistinct wall and only a few metrocytes. On day 45 sarcocysts were seen in the heart muscles and also in other unspecified organs. They were larger (65 x 17 μm) and contained more metrocytes but still had a poorly defined wall. They were not infective for a pup. On day 60 there were sarcocysts "in the muscles of different organs including heart." They were larger (473 x 34 μm), had a thick, radially striated wall and were partially mature but still noninfective for a pup. On day 92 a kid had many sarcocysts in the muscles of its esophagus, diaphragm, tongue and skeletal muscles but rarely in the heart. They were "mature" and infective for a pup. He thought that the sarcocysts in the heart were third-generation and those in the muscles of the other organs fourth-generation meronts.

Pethkar (1980) said that the sarcocysts in naturally infected goats

were elongate, with both ends tapering, lay within the muscle fibers, and were 583 μm long. Their wall was 3.7 μm thick and transversely striated. When immature they contained mostly oval or irregular metrocytes 9 x 4 μm. When mature they contained crescentic or banana-shaped bradyzoites 14 x 4 μm.

Gamogony. Pethkar (1980) saw gamonts in pups on days 1–5, and only oocysts from day 7 onward. Beginning on day 10 he found only fully sporulated oocysts and sporocysts. All stages were in the cells of the lamina propria of the anterior half of the small intestine.

Prepatent Period. 9–21 days in pups.

Patent Period. 28–70 days in pups.

Pathogenicity. Pethkar (1980) said that this species is highly pathogenic for goats. Kids fed 1,000,000 or 50,000 sporocysts from the dog became seriously ill with marked clinical signs leading to death 21–23 days after inoculation. He found inflammation and extensive hemorrhage in all organs that he examined histologically. He attributed these changes to meronts in the endothelial cells of the blood vessels. Three kids fed 25,000 sporocysts each had a slight increase in body temperature and then became normal. There were no lesions at 60 and 92 days.

Cross-Transmission Studies. Pethkar (1980) was unable to infect 5 kittens with sarcocysts from goats or 2 lambs with sporocysts from the dog.

Remarks. Although Pethkar (1980) called this species *S. moulei,* that species has macroscopic sarcocysts, whereas this does not, so it cannot be assigned to *S. moulei.* It is tentatively designated *Sarcocystis* sp. (Pethkar, 1980) nom. nov., although it may turn out to be *S. capracanis.*

Sarcocystis sp. Pethkar, 1980

Type Definitive Host. Dog *Canis familiaris.*

Type Intermediate Host. Domestic goat *Capra hircus.*

Location. Feces of dog; sarcocysts in skeletal muscles of goat.

Merogony. The sarcocysts in naturally infected goats are 574 x 104 μm and have a thin wall 1.0 μm thick with hair-like projections on its outer surface (Pethkar, 1980). Only mature sarcocysts were found. They contained crescent- or banana-shaped bradyzoites 14 x 4 μm.

Cross-Transmission Studies. Pethkar (1980) was unable to infect 2 kittens with sarcocysts from the goat.

***Toxoplasma gondii* (Nicolle and Manceaux, 1908) Nicolle and Manceaux, 1909**

Dubey (1981) found perinatal toxoplasmosis in goats on 2 farms in Montana. Of 7 pregnant does from 1 farm, 1 aborted a dead fetus and 2 had an infected kid *in utero*. He found *T. gondii* by mouse inoculation in 6 of these does, 4 of 4 cats, and 3 of 11 chickens on the farm. A pregnant doe on the second farm delivered 3 kids, of which 1 was dead, 1 moribund and 1 healthy. He isolated *T. gondii* from the placenta and all 3 kids. He (1981a) found that inoculation of pregnant goats with *T. gondii* oocysts caused reabsorption of the fetus, abortion or stillbirth. Two of 15 goats had normal kids, and 8 more had both stillborn and normal kids. The protozoa apparently invaded the fetal tissues 11–15 days after the pregnant goats had been fed sporocysts.

Dubey, Sundberg and Matiuck (1981) found *T. gondii* in an aborted goat fetus from Connecticut and in its placenta. They found antibodies in the mother and also in 4 adult goats, 8 sheep, 4 cats and 4 persons from the same farm.

Hartley and Seaman (1982) found what may have been *T. gondii* infection in the kidneys (and also some other organs) of a pregnant goat that died in Australia.

Dubey (1981f,g) found that oral vaccination of goats with 1 million oocysts of the nonpathogenic *Toxoplasma hammondi* or *T. heydorni* protected goats against subsequent inoculation with *T. gondii*.

For other information on *T. gondii*, see under the host species.

***Toxoplasma bahiensis* (de Moura Costa, 1956 emend. Levine, 1978) Levine, 1983**

See under *Bos taurus*.

***Besnoitia besnoiti* (Marotel, 1913) Henry, 1913**

Type Definitive Host. Cat *Felis catus*.

Type Intermediate Host. Ox *Bos taurus*.

Other Intermediate Hosts. Goats *Capra hircus, C. aegagrus* and other ruminants. The present discussion has to do only with the goat. For further information, see the discussion under *Bos*.

Location. Bwamgamoi (1968) found *Besnoitia* sp. in 2 of 29 goatskins plus 2 others in Kenya. Presumably it was *B. besnoiti*. Cheema and Toofanian (1979) found it in the skin, blood vessels, epididymis

and testes of 2 wild goats *C. aegagrus* and subcutaneous tissues of 2 domestic goats in Iran.

Host Genus *Ovis*

***Eimeria ahsata* Honess, 1942 emend. Levine and Ivens, 1970**
(Figs. 257–259, Levine and Ivens, 1970)

Synonym. Eimeria ah-sa-ta Honess, 1942.

Type Host. Rocky Mountain bighorn sheep *Ovis canadensis.*

Other Hosts. Domestic sheep *Ovis aries,* mouflon *O. musimon.* Reports of this species from *Capra* were probably of *E. christenseni* or *E. arloingi.*

Location. Small intestine.

Oocyst Structure. Ellipsoidal to somewhat ovoid, slightly flattened at the micropylar end, which is almost always the smaller one, 23–48 x 17–30 μm, with smooth, lavender to pinkish yellow to light brown, 2-layered wall 0.9–1.3 μm in total thickness, the outer layer accounting for almost the whole thickness, and the inner layer of intact oocysts appearing simply as a dark line on the inner surface of the wall and sometimes being somewhat wrinkled at the micropylar end, with micropyle, with dome-shaped micropylar cap, ordinarily with 1 or occasionally more polar granules, without residuum. Sporocysts 10–22 x 6–10 (mean 18 x 9) μm, without a Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with 1–3 clear globules each.

Merogony. The meronts occur mostly in the central part of the mucosa of the small intestine, most being in the jejunum; a few occur in the lacteals of the villi and a very few in the muscularis mucosae (Davis, Bowman and Smith, 1963). Fifteen days after inoculation they average 184 x 165 μm and range up to 265 x 162 μm. The host wall around the meronts is up to 9 μm thick; the larger the meront, the thinner the wall. The outer wall of the host membrane around young meronts is fimbriated, with radially arranged fibril-like strands as long as 13 μm.

Gamogony. Davis, Bowman and Smith (1963) first saw gamogony 12 days after inoculation. The macrogametes are 35–45 μm and the microgamonts about 26 x 36.5 μm. The gamonts and oocysts are mostly in the columnar epithelial cells lining the intestinal glands.

Prepatent Period. Eighteen to 20 days (Smith, Davis and Bowman, 1960).

Patent Period. 10–12 days (Smith and Davis, 1965).

Pathogenicity. Smith, Davis and Bowman (1960) considered this species the most pathogenic of all sheep coccidia. They produced fatal infections in 4 out of 9 lambs 1–3 months old by feeding them 100,000 oocysts. The intestines of the infected lambs had thickened, somewhat edematous areas in the upper part. The Peyer's patches and the last 20–25 cm of the small intestine above the ileocecal valve were inflamed.

Mahrt and Sherrick (1965) described an outbreak of coccidiosis in Illinois feeder lambs in which *E. ahsata* was the principal cause of death. Four flocks containing 2,000 lambs imported from Texas were crowded into feedlots; 33–40% had diarrhea, inappetence and depression. Weight loss was a prominent sign, and lambs that recovered did not gain weight well. About 4–6% of the lambs died.

Cross-Transmission Studies. Krylov (1961) could not transmit this species from the sheep to the goat.

***Eimeria ammonis* Musaev, 1970**

Synonym. Eimeria faurei (Moussu and Marotel, 1902) Martin, 1909 of Svanbaev (1958) in *Ovis ammon.*

Type Host. Argali *Ovis ammon.*

Oocyst Structure. Ovoid or short ovoid, 20–29 x 19–24 (mean 25 x 21) μm, with smooth, "double-contoured," yellow-green, orange-brown or brown wall 1.2–1.6 μm thick, with micropyle, sometimes with micropylar cap. Sporocysts ovoid or short ovoid, 5–12 x 5–9 (mean 8 x 6) μm, with residuum. Sporozoites 5–8 x 2–4 (mean 6 x 3) μm.

Cross-Transmission Studies. Svanbaev (1967, 1979) could not transmit this species from *O. ammon* to the goat or to lambs.

***Eimeria arkhari* Yakimoff and Matschoulsky, 1937**

(Fig. 60, Levine and Ivens, 1970)

Type Host. Arkhar or urial *Ovis vignei.*

Other Hosts. Ovis ammon polii and argali *O. a. sewerzowi.*

Oocyst Structure. Ellipsoidal, often ovoid, with double-contoured wall (illustrated as composed of 1 layer) up to 1 μm thick, sometimes yellowish, 20–24 x 18–20 (mean 22 x 17) μm, without micropyle, polar granule or residuum. Sporocysts ellipsoidal, 6–8 x 6 μm, without residuum. Sporozoites sausage-shaped.

Cross-Transmission Studies. This species cannot be transmitted from the sheep to the goat, saiga, roe deer or gazelle (Krylov, 1961; Lotze et al., 1961; Tsygankov, Paichuk and Balbaera, 1963; Svanbaev, 1979).

***Eimeria marsica* Restani, 1971** (Fig. 330)

Type Host. Domestic sheep *Ovis aries.*

Oocyst Structure. Ellipsoidal, 15–22 x 11–15 (mean 19 x 13) μm, with smooth, colorless to slightly grayish or pale yellow, 2-layered wall 0.5–1.0 μm thick, with micropyle, with or without micropylar cap, with or without polar granule, without residuum. Sporocysts ovoid, 7–11 x 4–7 (mean 8–10 x 5) μm, with small or no Stieda body, with residuum. Sporozoites elongate, with one end rounded and the other pointed, lying lengthwise head to tail in sporocyst, with a single small clear globule.

Prepatent Period. Fourteen to 15 days (Restani, 1971).

Pathogenicity. Probably slight. Norton and Catchpole (1976) saw no signs in a lamb given 10,000 oocysts, whereas Restani (1971) reported no pathogenic effects in two 30-day-old lambs given 50,000 oocysts each.

***Eimeria bakuensis* Musaev, 1970**

(Figs. 250, 254–256, Levine and Ivens, 1970)

Synonyms. Eimeria arloingi forma *ovina* Krylov, 1961; *E. arloingi* of auctores from sheep; *E. faurei* (Moussu and Marotel, 1902) of Yakimoff, 1931a, and of some other authors; *E. hawkinsi* Ray, 1952 in part (reports from sheep); *E. ovina* Levine and Ivens, 1970 [*non*] *E. arloingi* (Marotel, 1905) Martin, 1909; [*non*] *E. faurei* (Moussu and Marotel, 1902) Martin, 1909.

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Rocky Mountain bighorn sheep *Ovis canadensis,* argali *O. ammon,* mouflon *O. musimon.*

Location. Small intestine.

Oocyst Structure. Ellipsoidal to ovoid, generally with rather straight sides, slightly flattened at the micropylar end, 23–36 x 15–24 μm, with 2-layered wall, outer layer smooth, greenish or yellow-brown to orange, about 1.0–1.3 μm thick, inner layer a brownish-yellow membrane to black line up to 0.5 μm thick, with micropyle, with micropylar cap, with 1 or more polar granules (sometimes as

small shattered particles), without residuum. Sporocysts ovoid, 11–17 x 6–9 μm, with or without inconspicuous Stieda body, with residuum. Sporozoites elongate, with one end rounded and the other tapered, lying lengthwise head to tail in sporocysts, with a large clear globule at one end and a smaller one at the other end.

Merogony. The sporozoites emerge from the oocysts in the small intestine, enter the crypts of Lieberkuehn, and penetrate through the tunica propria into the interior of the villi. Here they enter the endothelial cells lining the central lacteals and grow. The host cell also grows, and its nucleus becomes very large. There is apparently only 1 generation of meronts and merozoites. The meronts become mature 13–21 days after inoculation. At this time they are about 122–146 μm in diameter and contain a large number (perhaps hundreds of thousands) of merozoites about 9 x 2 μm (Lotze, 1953).

Gamogony. Occurs in the epithelial cells of the small intestine villi. Some of the merozoites become microgamonts; these form many microgametes, leaving a large mass of residual material. Most of the merozoites become macrogametes. Following fertilization, the macrogametes turn into oocysts, which break out of the host cells and are first seen in the feces 20 days after inoculation (Lotze, 1953).

Prepatent Period. Nineteen–29 days (Lotze, 1953; Norton, Joyner and Catchpole, 1974).

Pathogenicity. Mildly pathogenic. Lotze (1952) found that 1 million oocysts or less produced no visible signs. In lambs inoculated with 3 or 5 million oocysts, the feces became soft on the 13th day and then returned to normal during the next 6 days. The health, general condition and weight gains of these animals were not affected. Severe diarrhea was produced beginning on day 15 with higher doses, but none of the animals died although one was killed in extremis. Blood-tinged mucus was passed by affected lambs only occasionally. The feces began to return to normal on the 17th day and were usually nearly normal by the 20th day. Lambs with marked diarrhea became weak and refused feed.

At necropsy, only a few small, slightly hemorrhagic areas scattered throughout the lining of the small intestine were seen up to the 13th day. From the 13th to 19th days the small intestine was more or less thickened and edematous, and thick, white opaque patches made up of groups of heavily parasitized villi were present.

The villi containing the meronts become thin-walled sacs and are

presumably destroyed. The sexual stages are clustered in the epithelial cells of the villi and destroy these cells when they emerge. However, they do not do as much damage as the asexual stages, because the condition of affected animals appears to improve before oocysts are shed. See also Chapman, Lewis and Searle (1973).

Immunity. Norton, Joyner and Catchpole (1974) found that this species is immunologically distinct from *E. weybridgensis.*

Cross-Transmission Studies. E. bakuensis cannot be transmitted from sheep to goats, saigas, roe deer or gazelles (Krylov, 1961; Lotze et al., 1961, 1964; Tsygankov, Paichuk and Balbaeva, 1963; Svanbaev, 1969; Sayin, Dincer, and Milli, 1980).

Remarks. According to Musaev in a letter dated February 5, 1985 to C. C. Norton, the publication date of *E. bakuensis* was October 1970. That of *E. ovina* was November 12, 1970. Hence, the latter name is a synonym of the former.

***Eimeria caprovina* Lima, 1980**

Type Host. Domestic goat *Capra hircus.*

Other Hosts. Domestic sheep *Ovis aries* (experimental).

Remarks. This species has been described above under *Capra.* Lima (1980) transmitted it from the goat to sheep and back to goats.

***Eimeria crandallis* Honess, 1942**

(Figs. 260, 261, 264, Levine and Ivens, 1970)

Type Host. Rocky Mountain bighorn sheep *Ovis canadensis.*

Other Hosts. Domestic sheep *Ovis aries,* mouflon *O. musimon,* argali *O. ammon.* In addition, this species has been reported from *Capra, Capreolus, Cervus, Dama, Rupicapra,* and *Gazella.* The reports from goat were most probably of *E. hirci.* It is extremely dubious that *E. crandallis* occurs in ruminants other than *Ovis.*

Location. Small intestine, extending anteriorly from the ileocecal valve (Pout, 1965, 1974a).

Oocyst Structure. In *O. canadensis,* ellipsoidal, 17.5–23 x 17.5–22 (mean 22 x 19) μm, with micropylar cap, with colorless, faint pink or greenish wall, with polar granule, apparently without residuum. Sporocysts 8–11 x 5–8 (mean 10 x 6) μm (Honess, 1942).

In *O. aries,* oocysts subspherical to broadly ellipsoidal, with slightly narrower micropylar end, 18–28 x 15–20 (mean 22 x 18) μm, with smooth, 2-layered wall, outer layer colorless, 0.9–1.3 (mean 1.1) μm

thick, inner layer a darkish yellow membrane lining the inner surface, slightly wrinkled at micropylar end, with distinct to indistinct micropyle, with colorless, flat to saucer-shaped micropylar cap, usually with 1 or more, often shattered, polar granules, without residuum. Sporocysts broadly ovoid with one end pointed, sometimes blunt, 8–13 x 6–9 (mean 11 x 7) μm, without Stieda body, with or without residuum. Sporozoites at ends of sporocysts, transverse, with 1 or 2 clear globules (Kamalapur, 1961).

Prepatent Period. Thirteen to 20 days (Pout, 1965; Norton, Joyner and Catchpole, 1974; Pout, Norton and Catchpole, 1973).

Patent Period. Four to 9 days (Pout, Norton and Catchpole, 1973).

Pathogenicity. Pout (1974b) found that doses of 2,500–250,000 *E. crandallis* oocysts per day for 7 days had no significant effect on milk intake by lambs but did decrease concentrate intake and daily weight gains during the next 29 days. A dose of 2,500 oocysts per day for 7 days produced 69–3,084 million oocysts; a dose of 10,000 oocysts per day for 7 days produced 74–1,376 million oocysts; and a dose of 250,000 oocysts per day for 7 days produced 629–853 million oocysts. He concluded that "no obvious relationship existed between the infective dose, the faecal oocyst production and the clinical response."

Immunity. Norton, Joyner and Catchpole (1974) differentiated this species from *E. ovina* by cross-infection experiments.

Cultivation. DeVos, Hammond and Speer (1972) cultivated *E. crandallis* in cell culture, beginning with sporozoites and obtaining first-generation meronts and merozoites. Bovine liver cell culture gave the best results. The mature meronts were up to 150 μm in diameter and were first seen 11–14 days after inoculation. Merozoites were formed by budding from the surface as well as from blastophores. The parasites injured the host cells. Complete development (i.e., oocyst formation) did not occur in any cell cultures.

Cross-Transmission Studies. Krylov (1961) was unable to infect two 3-month-old kids with *E. crandallis* from sheep.

***Eimeria dalli* Clark and Colwell, 1974** (Fig. 340)

Type Host. Dall sheep *Ovis dalli.*

Oocyst Structure. Spherical or subspherical, 38–47 x 36–42 (mean 44 x 37) μm, with rough, irregular, 3-layered wall, outer layer yellowish brown, 2–4 μm thick, middle layer colorless, about 0.5 μm thick,

inner layer colorless, about 0.5 μm thick, without micropyle or residuum, sometimes with polar granule. Sporocysts elongate ovoid, 16–21 x 10–12 (mean 19 x 11) μm, without Stieda body, with residuum. Sporozoites with one end broader than the other, lying lengthwise head to tail in sporocysts, with large clear globule at broad end and usually a smaller one at the narrow end.

***Eimeria danielle* Dida, 1970**

Type Host. Domestic sheep *Ovis aries.*

Remarks. This species was named and described in an unpublished thesis. We have seen no publication describing it and have not seen the thesis. We do not know whether this name is a synonym of some other one, and simply list it here without prejudice. Dida, Acsinte and Purcherea (1972) said that they had found it in 20% of an unspecified number of sheep in Romania. The only other species they mentioned as having been seen were *E. ahsata, E. arloingi, E. intricata* and *E. parva.*

***Eimeria faurei* (Moussu and Marotel, 1902) Martin, 1909**
(Figs. 231, 233, Levine and Ivens, 1970)

Synonyms. Coccidium faurei Moussu and Marotel, 1902; *C. ovis* Jaeger, 1921; *Eimeria aemula* Yakimoff, 1931; *E. ovis* (Jaeger, 1921) in the sheep.

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Rocky Mountain bighorn sheep *Ovis canadensis,* argali *O. ammon polli, O. a. sewerzowi,* mouflon *O. musimon,* Asia Minor mouflon *O. orientalis.* In addition, this species has been reported from *Ammotragus, Rupicapra, Capreolus, Dama* and *Ovibos.* Infections in these genera are undoubtedly of other species.

Location. Small (large ?) intestine.

Oocyst Structure. Ovoid, with micropylar, narrow end slightly flattened, 25–37 x 18–28 μm, with smooth, faint green, greenish yellow, pale yellowish brown, delicate salmon pink, or pale yellowish pink, 1-layered wall 1.3–1.8 μm thick, lined by a membrane, with conspicuous micropyle 2–3 μm in diameter, without micropylar cap, with polar granule, without residuum. Sporocysts ovoid or piriform, 11–17 x 7–9 (mean 14–15 x 8) μm, without Stieda body or with an inconspicuous one, with residuum. Sporozoites elongate, lying lengthwise

head to tail in sporocysts, with 1 or 2 large clear globules in each sporozoite.

Merogony. Uncertain.

Prepatent Period. Twelve to 14 days (Svanbaev, 1967a).

Pathogenicity. E. faurei is only mildly pathogenic. Lotze (1954) found that single inoculations of 3-month-old lambs with 5 million oocysts produced only a temporary softening of the feces without significantly affecting the health or physical condition of the animals. Inoculation of 50 million oocysts failed to cause death. Svanbaev (1967a) reported signs in 2 out of 4 40-day-old lambs given 10,000 oocysts each. They had diarrhea, inappetence, depression, anemia, conjunctivitis and gained weight poorly. Inflammation, hyperemia and gray-white nodules were present in the duodenum and rarely the jejunum and ileum.

Cross-Transmission Studies. This species cannot be transmitted from the sheep to the Norway rat (Becker, 1933), saiga, roe deer, or apparently goat (Krylov, 1961; Lotze et al., 1961; Tsygankov, Paichuk and Balbaeva, 1963; Svanbaev, 1979).

***Eimeria gonzalezi* Bazalar and Guerrero, 1970**

(Fig. 291, Levine and Ivens, 1970)

Synonym. Eimeria sp. Patyk, 1965.

Type Host. Domestic sheep *Ovis aries.*

Oocyst Structure. Ellipsoidal or ovoid, 26–38 x 18–26 μm, slightly flattened at micropylar end, with smooth, 2-layered wall 1–2 μm thick, outer layer transparent, inner layer yellowish brown, with a micropyle and a micropylar cap, with polar granule, without residuum. Sporocysts ovoid, 12–15 x 6–9 (mean 14 x 8) μm, with slightly perceptible Stieda body, with residuum. Sporozoites with 2–3 clear globules each.

***Eimeria granulosa* Christensen, 1938**

(Figs. 246, 247, Levine and Ivens, 1970)

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Rocky Mountain bighorn sheep *Ovis canadensis,* mouflon *O. musimon.* This species has also been reported from *Capra* and *Ovibos,* but the former is *E. jolchijevi* and the latter attribution is dubious (see above).

Oocyst Structure. Piriform, ellipsoidal or urn-shaped, 22–37 x 17–

26 μm, with a smooth, 2-layered wall, outer layer pale and 0.4–0.6 μm thick, inner layer darker and 0.8 μm thick, lined by a membrane, with a micropyle and micropylar cap at the *broad* end, with or without polar granules, without residuum. Sporocysts ovoid or elongate ovoid, rounded at both ends, 13–16 x 8–9 μm, with faintly perceptible Stieda body and residuum. Sporozoites elongate, with one end wider than the other, lying lengthwise head to tail in sporocysts, with 1–3 clear globules.

Cross-Transmission Studies. Krylov (1961) could not infect the goat with this species from sheep.

***Eimeria intricata* Spiegl, 1925**

(Figs. 235–238, 271, Levine and Ivens, 1970)

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Rocky Mountain bighorn sheep *Ovis canadensis,* mouflon *O. musimon.* This species has also been reported from *Capra, Capreolus* and *Dama.* Whether it actually occurs in hosts other than *Ovis* is dubious (see above under *E. kocharii).* The following discussion pertains only to *Ovis.*

Location. Meronts in lower small intestine. Gamonts and oocysts in small intestine posteriorly to the rectum, with most in the cecum. Both meronts, gamonts and oocysts are in epithelial cells lining the crypts. The largest meronts seen by Lotze and Leek (1970) were about 75 x 37.5 μm (in the glands of Lieberkuehn on day 17). They counted 400 meronts in a single gland on day 11 (Davis and Bowman, 1965; Pande, Bhatia and Chauhan, 1966; Michael and Probert, 1970).

Oocyst Structure. Ellipsoidal or slightly ovoid, 35–59 x 27–47 μm, with 2-layered wall, outer layer irregular, granular, brownish yellow to dark brown, 2–3 μm thick, transversely striated and appearing divided into 2 sublayers by a faint line, inner layer dark brown, 0.4–0.8 μm thick, lined by a membrane which is often wrinkled at the micropylar end, with micropyle in outer layer only, with prominent, detachable micropylar cap, generally with 1 or more polar granules, without residuum. Sporocysts elongate ovoid, with one end bluntly pointed, 17–22 x 9–14 (mean 20 x 11) μm, without Stieda body or with extremely tiny one, with residuum. Sporozoites elongate, with one end narrower than the other, lying lengthwise head to tail in sporocysts, with 2–3 clear globules.

Merogony. The meronts occur in the small intestine, mostly in the cells lining the intestinal crypts. There are apparently 2 generations, the first being mature by day 7 and the second by day 17 (Lotze and Leek, 1970). The largest that Davis and Bowman (1965) found was 65 x 45 μm and contained large merozoites up to 19.5 x 4 μm; the size of the merozoites gave the meronts a granular appearance. The largest meronts that Lotze and Leek (1970) saw were about 75 x 37.5 μm (on day 17). Their merozoites were about 12 x 1.7 μm. They counted 400 meronts in a single gland on day 11.

Gamogony. Gamonts and oocysts occur from the small intestine posteriorly to the rectum, with most in the cecum. They are in the cells lining the intestinal crypts. The microgamonts are spherical to elongate, 52 x 34 μm, and contain slender, flagellated microgametes; the macrogametes are spherical to ovoid, 32 x 29 μm.

Prepatent Period. Twenty to 27 days (Davis and Bowman, 1965; Krylov, 1961; Svanbaev, 1967a; Bhatia, Ahluwalia and Chauhan, 1972).

Patent Period. Five to 11 days (Davis and Bowman, 1965; Svanbaev, 1967; Bhatia, Ahluwalia and Chauhan, 1972).

Pathogenicity. Oocysts of this species are rarely found in large numbers, and it is apparently not very pathogenic (Svanbaev, 1967a).

***Eimeria ovinoidalis* McDougald, 1979**

(Figs. 227, 229, 230, Levine and Ivens, 1970)

Synonym. Eimeria ninakohlyakimovae Yakimoff and Rastegaieff, 1930 emend. Levine, 1961 of *auctores* (from sheep); *E. galouzoi* Yakimoff and Rastegaieff, 1930 in part; *E. ovis* Musaev, 1970; [*non*] *E. ovis* Jaeger, 1921.

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Rocky Mountain bighorn sheep *Ovis canadensis,* mouflon *O. musimon.*

Location. Small intestine, especially the posterior part, and also cecum and colon.

Oocyst Structure. Ellipsoidal or subspherical to somewhat ovoid, 16–30 x 13–22 μm, with 2-layered wall, outer layer smooth, colorless to slightly greenish, 1 μm thick, inner layer yellowish brown, 0.4 μm thick, wall lined by a membrane often wrinkled at micropylar end, with micropyle at small end, without micropylar cap, ordinarily with

2 or more polar granules, without residuum. Sporocysts elongate ovoid, 10–14 x 4–8 μm, with Stieda body and residuum. Sporozoites elongate 11.5–14 x 2–4 (mean 13 x 3) μm, lying lengthwise head to tail in sporocysts, with 1 large and 1 small clear globule.

Merogony. The sporozoites enter the epithelial cells at the base of the glands of Lieberkuehn in the small intestine; there they form meronts about 300 μm in diameter, which contain thousands of merozoites (Lotze, 1954).

There are 2 generations of meront; the first generation develop in cells of the lamina propria adjacent to the base of the posterior small intestine. They become mature 9 days after inoculation, at which time they have an average diameter of about 290 μm and contain many thousands of merozoites averaging 12 x 2 μm. The merozoites are produced by ectopolygeny from spherical blastophores which form within the meronts. Second-generation meronts occur in epithelial cells lining the crypts of the large intestine. They become mature 10–11 days after inoculation, have a mean diameter of about 12 μm and contain a mean of 24 merozoites which average 5.5 x 1.4 μm (Wacha, Hammond and Miner, 1971).

Gamogony. Microgamonts and macrogametes occur in the epithelial cells of the ileum, cecum and upper part of the large intestine, appearing 11–15 days or more after inoculation. The mature microgamonts average 15 x 12 μm and have microgametes arranged peripherally about a central residuum. The mature macrogametes average 16 x 12 μm, and the oocysts 18 x 13 μm (Lotze, 1954; Wacha, Hammond and Miner, 1971).

Prepatent Period. Nine to 15 days (Shumard, 1957a; Krylov, 1961; Svanbaev, 1967a; Hammond, Kuta and Miner, 1967; Wacha, Hammond and Miner, 1971; McDougald, 1979).

Patent Period. Seven to 18 days (Svanbaev, 1967a; Hammond, Kuta and Miner, 1967; Wacha, Hammond and Miner, 1971).

Pathogenicity. This is one of the most pathogenic of sheep coccidia. Lotze (1954) found that as few as 50,000 oocysts caused diarrhea in a 3-month-old lamb; as few as 500,000 oocysts caused death. He produced dysentery in a 2-year-old sheep by inoculation with 1 million oocysts. He found that the feces of experimentally infected lambs became soft in 12–17 days. They became watery a day or 2 later and remained so for a week or more. The feces of the more heavily in-

fected lambs contained blood-stained mucus beginning 15 days after inoculation or soon thereafter. The feces of animals that recovered remained soft for some weeks.

Smith and Davis (1965) found that only 20,000 oocysts caused death and only 10,000 caused clinical signs in lambs if the oocysts were given in dry feed rather than in liquid.

Chapman (1974) found that inoculation of 100,000 oocysts of an English strain caused severe signs and death in half of lambs about 2 months old. Diarrhea began about 4 days after inoculation and continued for about 8 days, at which time it ceased and "was replaced by considerable straining and the exudation of a clear liquid." The lambs died 14–18 days after inoculation. There was no loss of blood, and indeed both hemoglobin and hematocrit increased, indicating hemoconcentration. There was no significant change in serum protein, but serum albumin decreased and serum globulin increased. Surviving lambs had decreased weight gains.

Bergstrom and Maki (1976) found in Wyoming that 18,000 sporulated oocysts produced severe clinical coccidiosis with diarrhea and rapid weight loss in lambs averaging 37.3 kg.

Others who have reported on the pathogenicity of this species are Svanbaev (1967a,b), Hammond, Kuta and Miner (1967) and Shumard (1957b).

Immunity. Chapman (1974a) found that previous inoculation with 50,000 oocysts immunized lambs against subsequent inoculation with 200,000 oocysts. Betamethasone partially suppressed the development of immunity to natural infection.

Cross-Transmission Studies. This species cannot be transmitted from sheep to goats, saigas, roe deer or gazelles (Krylov, 1961; Lotze et al., 1961, 1964; Tsygankov, Paichuk and Balbaeva, 1963; McDougald, 1979; Svanbaev, 1979).

Cultivation. Kelley and Hammond (1970, 1972, 1973) cultivated this species in monolayer cell line cultures of sheep trachea, thyroid, thymus and kidney cells as well as in an established Madin-Darby cell line of bovine kidney cells. They got best results with sheep kidney and trachea cells.

***Eimeria pallida* Christensen, 1938**

(Figs. 248, 249, Levine and Ivens, 1970)

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Domestic goat *Capra hircus,* ibex *C. ibex.* The following discussion refers only to the sheep.

Oocyst Structure. Ellipsoidal, 12–20 x 8–15 μm, with smooth, colorless to very pale yellow or yellowish green, 2-layered wall 0.5 μm in total thickness, outer layer accounts for almost the whole wall thickness, inner layer appears simply as a dark line on the inner surface of the wall, without perceptible micropyle, without micropylar cap, with or without polar granule, without residuum. Sporocysts elongate ovoid, 6–9 x 4–6 μm, without Stieda body, with residuum. Sporozoites elongate, usually lying lengthwise head to tail in sporocysts, but often with a tendency to lie crosswise in them, with a single clear globule.

Remarks. It is possible that this name actually refers to different species in the sheep and goat.

***Eimeria parva* Kotlan, Mocsy and Vajda, 1929**
(Figs. 239, 242–244, Levine and Ivens, 1970)

Synonym. Eimeria galouzoi Yakimoff and Rastegaieff, 1930 in part.

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Mouflon *Ovis orientalis,* argali *O. ammon,* mouflon *O. musimon,* Rocky Mountain bighorn sheep *O. canadensis.* In addition, this species has been reported from *Capra, Ammotragus, Capreolus, Cervus, Dama,* and *Rupicapra.* However, these reports are either erroneous (Pellérdy, 1965, 1974) or dubious. *E. "parva"* of goats is actually *E. alijevi* (see above).

Location. The meronts occur in the small intestine and the sexual stages mostly in the cecum and colon and to a lesser extent in the small intestine.

Oocyst Structure. Subspherical, ovoid, ellipsoidal or spherical, 12–23 x 10–19 μm, with smooth, pale yellow to yellowish green, brownish yellow or faint pinkish mauve, 2-layered wall, outer layer 0.8–1.2 μm thick and thinning at micropylar end, inner layer a dark, thin membrane, with inconspicuous micropyle, without micropylar cap, generally with polar granule, without residuum. Sporocysts ovoid, 6–13 x 5–8 μm, without Stieda body or with a small one, with residuum composed of a few fine granules. Sporozoites with 1 clear globule.

Oocysts in Rocky Mountain bighorn sheep similar to those in the domestic sheep but larger, 17–24 x 17–22 (mean 20 x 19) μm (Honess, 1942).

Merogony. Kotlán, Pellérdy and Versényi (1951a, 1951b) described the endogenous stages in sheep. However, it is not certain whether they were actually dealing with *E. parva* alone. They found meronts up to 185–256 x 128–179 μm, easily visible to the naked eye as whitish bodies throughout the small intestine. They lay in the mucosa, usually near the surface but sometimes as far down as the muscularis mucosae. Each meront produced thousands of straight merozoites 10–12 μm long.

A second, much smaller type of meront was also present in the small intestine. It occurred in the superficial epithelial cells, was 10–12 μm in diameter, and contained about 10–20 merozoites 2.5–3.0 μm long. Kotlán, Pellérdy and Versényi (1951) were not sure whether these were part of the life cycle of *E. parva.*

Gamogony. The sexual stages occur mostly in the cecum and colon and, to a lesser extent, in the small intestine. They are in epithelial cells and are 15–19 x 10–16 μm (Kotlán, Pellérdy and Versény, 1951).

Prepatent Period. Eleven to 15 days (Krylov, 1961; Svanbaev, 1967a).

Pathogenicity. E. parva is apparently not very pathogenic in sheep. Most of the damage is caused by the sexual stages in the large and small intestines.

Cross-Transmission Studies. E. parva cannot be transmitted from sheep to goats, roe deer, or gazelles (Krylov, 1961; Tsygankov, Paichuk and Balbaeva, 1963; Fitzsimmons, 1964; Svanbaev, 1967, 1979).

Eimeria punctata Landers, 1955

(Figs. 231, 252, Levine and Ivens, 1970)

Synonyms. Eimeria honessi Landers, 1952, [*non*] *E. honessi* Alderson, 1951 *nomen nudum,* [*non*] *E. media* var. *honessi* Carvalho, 1943.

Type Host. Domestic sheep *Ovis aries.*

Other Host. Domestic goat *Capra hircus.* The following discussion refers only to *Ovis.* It is suspected that the forms in *Ovis* and *Capra* are actually different species.

Oocyst Structure. Ellipsoidal or subspherical to ovoid, slightly flattened at micropylar end, 18–28 x 16–21 μm, with 2-layered wall having conspicuous, uniform, cone-shaped pits about 0.4–0.5 μm in diameter, outer layer 1.4 μm thick, colorless to yellowish, inner layer 0.4 μm thick, greenish to brownish yellow, with micropyle at small end of oocyst, with imperceptible to prominent, colorless, cone-

shaped micropylar cap, ordinarily with polar granule, usually with residuum. Sporocysts ovoid or piriform, 12–15 x 7–9 μm, with faintly perceptible Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with a single clear globule at one end.

***Eimeria rachmatullinae* Svanbaev, 1979**

Synonym. Eimeria arloingi (Marotel, 1905) Martin, 1909 of Svanbaev (1969) in *Ovis ammon.*

Type Host. Argali *Ovis ammon.*

Oocyst Structure. Ellipsoidal to ovoid, 22–35 x 18–21 (mean 28 x 20) μm, with smooth, yellow-brown, "double-contoured" wall 1.2–1.5 μm thick, with micropyle and micropylar cap, without residuum or polar granule. Sporocysts ellipsoidal, 8–13 x 5–9 (mean 11 x 7) μm, apparently without Stieda body, with residuum. Sporozoites 6–8 x 2–5 (mean 7 x 4) μm.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species from *O. ammon* to 13 *O. aries* lambs or 9 *Capreolus capreolus.*

***Eimeria surkovae* Musaev, 1970**

Synonym. Eimeria ninakohlyakimovae Yakimoff and Rastegaieff, 1930 of Svanbaev (1958) in *Ovis ammon.*

Type Host. Argali *Ovis ammon.*

Oocyst Structure. Ovoid or spherical, 19–28 x 18–27 (mean 25 x 22) μm, with smooth, yellowish, yellow-green or yellow-brown, "double-contoured" wall 1.1–2.3 μm thick. Sporocysts ovoid to spherical, 8–12 x 6–8 (mean 10 x 7) μm, with residuum. Sporozoites 5–8 x 3–4 (mean 7 x 3) μm.

Cross-Transmission Studies. Svanbaev (1979) could not infect 32 domestic lambs or 9 *Capreolus capreolus* with this species.

***Eimeria weybridgensis* Norton, Joyner and Catchpole, 1974** (Fig. 341)

Synonym. Eimeria arloingi "B" of Pout, Norton and Catchpole, 1973.

Type Host. Domestic sheep *Ovis aries.*

Location. Small intestine, chiefly jejunum (Pout, 1974).

Oocyst Structure. Broadly ellipsoidal to subspherical, 17–31 x 14–19 (mean 24 x 17) μm, with 2-layered wall, outer layer usually smooth

but occasionally slightly roughened, about 1 μm thick, colorless or pale yellow, inner layer a thin, dark membrane, with micropyle, with shallow, dome-shaped, colorless micropylar cap, with polar granule, without residuum. Sporocysts ovoid, 13–15 x 6–8 (mean 14 x 7) μm, without Stieda body, with residuum. Sporozoites elongate, lying lengthwise head to tail in sporocysts, with clear globule at each end.

Prepatent Period. 23–33 days (Pout, Norton and Catchpole, 1973; Norton, Joyner and Catchpole, 1974).

Patent Period. Nine to 12 days (Pout, Norton and Catchpole, 1973; Norton, Joyner and Catchpole, 1974).

Pathogenicity. Pout (1974a) found that a dose of 10,000 *E. weybridgensis* oocysts per day for 7 days did not significantly affect milk intake, concentrate intake or daily weight gain during the next 29 days in lambs. Totals of 78 to 4,388 million oocysts were produced during this period. Hence this species is only slightly if at all pathogenic.

Immunity. Norton, Joyner and Catchpole (1974) found that this species is immunologically distinct from *E. bakuensis.*

***Eimeria zejnijevi* Musaev, 1970**

Synonym. Eimeria intricata Spiegl, 1925 of Svanbaev (1958) in *Ovis ammon.*

Type Host. Argali *Ovis ammon.*

Oocyst Structure. Ovoid, 39–51 x 34–41 (mean 46 x 38) μm, with "tri-contoured," rough, yellowish brown to brown wall 3.5–4.3 μm thick, outer layer rough, inner radially striated, with micropyle and micropylar cap. Sporocysts ovoid, 12–20 x 8–13 (mean 15 x 10.5) μm, with residuum. Sporozoites 8–13 x 4–6 (mean 11 x 4.5) μm.

Cross-Transmission Studies. Svanbaev (1979) could not transmit this species from *O. ammon* to 44 domestic lambs, 17 kids, 12 young saigas or 24 *Capreolus capreolus,* although he did transmit it successfully to 4 young *O. ammon.*

***Eimeria gilruthi* (Chatton, 1910) Reichenow and Carini, 1937**

Synonyms. Gastrocystis gilruthi Chatton, 1910; *Globidium gilruthi* (Chatton, 1910) Nöller, 1920.

Type Host. Domestic sheep *Ovis aries.*

Other Hosts. Domestic goat *Capra hircus,* Siberian wild goat *C. sibirica.* In addition, Abdussalam (1953) found this organism in a wild

sheep *Pseudois nahoor (Ovis nahura)* that died in the Zoological Gardens at Lahore, Pakistan.

The following discussion includes both sheep and goats. See Remarks for a discussion of what this (or these) species might be.

Location. Abomasum wall.

Oocyst Structure. The oocysts of this (or these) species are unknown, only the meronts and merozoites having been seen (see below).

Merogony. The meronts occur in the connective tissue and mucous membranes of the abomasal wall. They are easily visible to the naked eye as whitish nodules and are 300–900 μm in diameter. Their wall is up to 40 μm thick. The host cell nucleus is flattened and greatly enlarged. The mature meronts contain thousands of crescent- to sickle-shaped merozoites which have been variously described as 4–16 μm long (see below).

The "cysts" have been described by Gilruth (1910), Triffitt (1925, 1928), Soliman (1960), Bhatia and Pande (1966), Pande and Bhatia (1966), Tontis, König and Hörning (1977) and Sarwar (1951), among others (see Levine and Ivens, 1970).

Porchet-Henneré (1977) studied the structure of meronts near maturity of *E. gilruthi* from the sheep abomasum in France. She said that the meronts are harbored by a highly differentiated host cell which is covered with long filiform evaginations and enclosed in a parasitophorous vacuole bearing short microvilli. It has a large nucleus and a dense layer of cytoplasmic microfibrils along its outer wall. The plasma membrane, accompanied by micropores, invaginates and forms deep tunnels which form internal vacuoles arranged in globular systems. These turn into large spherical vacuoles around which the nuclei are arranged in preparation for the last division. New "splits" across the parasite separate cytoplasmic masses of unequal size at the periphery of which nuclei undergo their last mitosis. Each pole of a dividing nucleus is the axis of a future merozoite. The merozoites are produced by budding. She apparently saw no metrocytes. She (1976) said that the merozoites have the standard apicomplexan organelles, including conoid, 2 rhoptries, micronemes, micropore and 22 transversely striated subpellicular microtubules; the striations were 4 nm apart. She also (1977a) described the formation of supernumerary conoids during merogony. This is an abnormal process, associated with apical rings, a short bundle of microtubules and little

rhoptries; she said that these conoids might have been induced by a nearby nucleus during development.

Hilali (1973) found 4 types of merozoite in "globidia" in the abomasa of 78% of 124 lambs and sheep slaughtered in Norway. He named them on the basis of merozoite size. The Small A type meronts were 342–701 x 212–527 (mean 481 x 352) μm with merozoites 4–5 x 1 (mean 4 x 1) μm. The Small B type were 279–645 x 180–439 (mean 436 x 327) μm, with merozoites 4–6 x 1–2 (mean 5 x 2) μm. The Intermediate type were 394–621 x 291–493 (mean 502 x 373) μm with merozoites 7–8 x 1–2 (mean 8 x 1) μm. The Long type were 422–711 x 341–623 (mean 584 x 459) μm with merozoites 7–10 x 1–2 (mean 9 x 1) μm. Small A merozoites were spindle-shaped, pointed at both ends, with a nucleus in the center. Small B merozoites were lanceolate, with a nucleus at one end. Intermediate merozoites were elongate fusiform, pointed at both ends, with a nucleus usually in the middle. Long merozoites were banana-shaped with pointed ends, with a nucleus at one end.

Hilali studied the fine structure of the Intermediate merozoites in detail. They have 2 polar rings, a 3-layered outer membrane, an inner membrane of the pellicle, 22 subpellicular microtubules, a conoid, 2 rhoptries, a rodshaped body between the rhoptries, an elongate, nearly central nucleus, a globular prenuclear body 0.7 μm in diameter, 20–50 oval bodies, many ribosomes, endoplasmic reticulum, mitochondria and a micropore. He thought that the Small A meronts might be a developing stage of the Intermediate form.

Mehlhorn and Heydorn (1976) found 2 types of giant meront ("Globidium") in the wall of the abomasum of sheep in Germany. Both had diameters of about 250 μm up to 500 μm. In Type 1 the zoites were ovoid, about 4 μm long and had 24 subpellicular microtubules. In Type 2 the zoites were spindle-shaped, about 6 μm long and had only 22 subpellicular microtubules. Both types had a vacuole 1.5–2 μm in diameter anterior to the nucleus. In this they differed from both *Eimeria* and *Sarcocystis*. The cytoplasm of both was subdivided into many spheroidal blastophores which were still present in old meronts. Their interior contained many nuclei, which later formed zoites.

The meronts had a thick, 2-layered wall. The inner layer was identical with the host cell cytoplasm and enclosed a giant parasitophorous vacuole. The outer surface of the host cell had numerous

microvilli up to 14 μm long. These microvilli and many macrophages scattered between them apparently formed the outer layer seen by light microscopy. The host cell itself was filled with many bundles of fibrillar origin, long rows of vacuoles and mitochondria, and seemed to be very dense. The inner surface of the host cell formed many intravacuolar tubules about 50 nm in diameter and 4 μm long.

They said that these globidial meronts differed clearly from sarcocysts.

Hilali and Scholtyseck (1979) found globidia in the abomasa of 93% of 30 lambs in Germany and studied their fine structure. They were in a parasitophorous vacuole in an intact host cell. They were either multinucleate giant meronts or contained developing or fully developed merozoites. The latter were of 2 types, short and long. The long ones were cylindrical, 7–9 x 1 (mean 8 x 1) μm, with a nucleus near the posterior end. The short ones were spindle-shaped, 5–6 x 1–2 (mean 5 x 1) μm, with a central nucleus. The multinucleate meronts were 239–394 x 200–259 μm, those containing long merozoites were 352–543 x 240–432 μm, and those containing short merozoites were 256–423 x 212–351 μm. In the process of merozoite formation, the giant meront nuclei divided repeatedly to form numerous multinucleate blastophores of irregular size and shape. Each blastophore contained about 6–50 nuclei, a unit membrane, well-developed endoplasmic reticulum, mitochondria, lipid droplets, and had 1 or more micropores. The nuclei became arranged at the periphery of the blastophores; the cytoplasm around them protruded, became covered with a 3-membraned pellicle, and formed merozoites by budding. The long merozoites had a conoid, polar ring(s), usually 2 rhoptries, numerous micronemes, 22 subpellicular microtubules, a micropore, a large ovoid body containing many granules, a relatively large, dense globule posterior to the micronemes, often 1 or 2 dark bodies, a nucleus, a mitochondrion and amylopectin granules. The short merozoites had the same organelles as the long ones but fewer micronemes and no dark bodies; they had a thick-walled vesicle posterior to the nucleus. There was sometimes a residuum in both types of meront.

These authors thought that the presence of the ovoid body in front of the nucleus seemed to differentiate these merozoites from those of *Eimeria* and *Sarcocystis*.

Various authors have described giant meronts (globidia) from the

small intestine of sheep and goats (and even from the cecum of sheep—Bhatia and Pande, 1966b). Tontis, König and Hörning (1977) found them in the small intestine of both sheep, goats and cattle. Whether they belong to the same species as the abomasal meronts is unknown.

Remarks. "*E. gilruthi*" may be the meront of one or more species of coccidia of the sheep and goat already known from the oocysts. However, we do not know what species it or they may be. Reichenow (1929) said that it was very probably *E. intricata*. Becker (1956) agreed and, since the name *E. gilruthi* has priority, synonymized *E. intricata* with it. However, Davis and Bowman (1965) later found that *E. intricata* does not have giant meronts, so this species cannot be *E. gilruthi*. Could it possibly be one or more species of *Sarcocystis*? Or a new genus?

Eimeria sp. Mincheva, Sherkov, Monov, Kyurtov, Bratanov, Meshkov and Donev, 1966

Type Host. Domestic sheep *Ovis aries*.

Oocyst Structure. Spherical to ellipsoidal, with thick, smooth, colorless wall, with prominent micropyle. Spherical oocysts 10 μm in diameter, ellipsoidal ones 10 x 6 μm. Sporocysts spherical. No other information given.

Isospora sp. Shah, 1963

(Fig. 266, Levine and Ivens, 1970)

Type Host. Domestic sheep *Ovis aries*.

Oocyst Structure. Usually subspherical, occasionally spherical, 20–25 x 20–24 (mean 23 x 22) μm, with 2-layered wall, outer layer smooth, pale yellowish or pale yellowish brown, 1 μm thick, inner layer brownish yellow, 0.5 μm thick, forming a thin membrane, without micropyle, micropylar cap or residuum, ordinarily with polar granule. Sporocysts lemon-shaped, quite thick-walled, 14–15 x 9–10 (mean 14 x 10) μm, with button-shaped Stieda body, with hyaline substiedal body, with residuum composed of fine granules. Sporozoites more or less sausage-shaped, not arranged in any particular order in sporocysts. There appeared to be a membrane within the sporocysts which enclosed both the sporozoites and sporocyst residuum so that they formed more or less of a ball.

Remarks. It is uncertain, as Shah (1963) said, whether this form is

actually a genuine parasite of the sheep or a pseudoparasite; it resembles the *Isospora* of house sparrows and was probably a feed contaminant passing thru the sheep.

***Isospora* sp. Golemanski, 1977**

In a survey of wild mouflons in Bulgaria, Golemanski (1977) found an *Isospora* sp. that he thought was probably passing through the intestine from a wild bird. Its oocysts were subspherical, 22–26 x 20–23 μm, with a micropyle, with a 2-layered wall, without a residuum or polar granule. Its sporocysts were ovoid, 15 x 10 μm, with a Stieda body and possibly with a residuum.

***Sarcocystis ferovis* Dubey, 1983**

Type Definitive Host. Coyote *Canis latrans.*

Type Intermediate Host. Bighorn sheep *Ovis canadensis.*

Location. Sarcocysts in bighorn sheep muscles. Oocysts and sporocysts in coyote intestine.

Oocyst Structure. Oocysts 20 x 14 μm, without micropyle, polar granule or residuum. Sporocysts 14 x 10 μm, ellipsoidal, without Stieda body, with residuum.

Merogony. Dubey (1983) said that the sarcocysts are microscopic, septate, with a smooth, thin wall 0.6 μm thick, and contain bradyzoites 10–14 x 3–3.5 μm.

Prepatent Period. 8 days in coyote.

Remarks. Dubey (1983) could not transmit this species to domestic sheep, goats or oxen.

***Sarcocystis gigantea* (Railliet, 1886) Ashford, 1977**

Synonyms. Balbiania gigantea Railliet, 1886; *Sarcocystis tenella* (Railliet, 1886) Moulé, 1886 of *auctores* in part; *S. ovifelis* Heydorn, Gestrich, Mehlhorn and Rommel, 1975; *Endorimospora tenella* (Railliet, 1886) Tadros and Laarman, 1976.

Type Definitive Host. Domestic cat *Felis catus.*

Other Definitive Hosts. Red fox *Vulpes vulpes,* possibly coyote *Canis latrans.*

Type Intermediate Host. Domestic sheep *Ovis aries.*

Other Intermediate Host. Rocky Mountain bighorn sheep *Ovis canadensis,* mouflon *O. musimon* (Kutzer and Hinaidy, 1969).

Location. Gamonts, gametes, zygotes, oocysts and sporocysts in

lamina propria of villi of small intestine of cat. Sarcocysts (meronts) in skeletal muscles of sheep, especially in wall of esophagus.

Oocyst Structure. Oocysts in parasitophorous vacuoles, mostly in posterior small intestine, about 15–18 x 10–14 μm, without micropyle. Most oocysts sporulated; the few unsporulated ones had a smooth, colorless, 1-layered wall about 0.25 μm thick; it shrank to 0.1 μm during sporulation. The oocysts apparently have no micropyle, residuum or polar granule. Sporocysts in intestinal wall 10–12 x 6–8 (mean 11 x 7) μm; in cat feces sporocysts 10–14 x 8–10 (mean 12 x 9) μm, with smooth, colorless wall, without Stieda body, with residuum. Sporozoites sausage-shaped, about 9 x 3 μm, with a clear globule at one end (Rommel, Heydorn and Gruber, 1972; Rommel, 1974; Munday and Richard, 1974; Mehlhorn, 1974; Mehlhorn and Scholtyseck, 1974; Sela Perez, 1979).

There is no merogony in the cat intestine and gamogony occurs in less than a day (Becker, Mehlhorn and Heydorn, 1979).

Merogony. It is not known whether there is an early generation of meronts in the visceral or other organs of sheep. The sarcocysts in sheep muscle are rather ellipsoidal and up to 1 cm long. They grow slowly, and few are found in sheep under 3 years of age in Australia (Munday and Rickard, 1974). It takes 8–14 months for them to become infective for cats. Their fine structure, and that of the bradyzoites within them was described in detail by Sénaud (1967), Mehlhorn and Scholtyseck (1973), Scholtyseck, Mehlhorn and Müller (1974), Porchet-Henneré and Ponchel (1974), Porchet-Henneré (1975), Mehlhorn, Hartley and Heydorn (1976), D'Haese, Mehlhorn and Peters (1977) and Sela Perez (1979), among others. The sarcocyst wall is composed of 2 distinct layers, a primary and a secondary wall (Mehlhorn and Scholtyseck, 1973). The secondary wall is composed of 2 layers; the outer is lamellar cytoplasm and within it is a layer of muscular tissue containing many nuclei and mitochondria in young sarcocysts. In larger sarcocysts the myofibrils are almost completely disintegrated. This wall is, of course, formed by the host cell. The primary wall delimits the sarcocyst proper, and is formed by the parasite. It is osmiophilic, about 25 nm wide, and has many villus-like folds and vesicle-like invaginations into the sarcocyst interior. The folds form cauliflower-like protrusions which contain microtubules. Beneath the primary sarcocyst wall is a zone of fine, granular ground substance which extends as septa into the interior of the sarcocyst, dividing it into compartments.

In the younger sarcocysts the periphery is occupied by metrocytes, which are globular, about 15–20 μm long, with a deeply invaginated pellicle. These cells have several micropores, a typical conoid, a polar ring with anchored subpellicular microtubules and a Golgi complex. Their nucleus has a nucleolus and a globular accumulation of electron-dense granules that are apparently not present in merozoites. Mehlhorn and Scholtyseck (1973) did not see rhoptries or micronemes, but others apparently have (see Scholtyseck, 1973). This last author said that "their major features are a deeply folded cell surface, a widely distributed system of vesicles and lacunae in the cytoplasm, and a nucleolus surrounded by a spiral structure, which resembles that of a chromosome."

Sénaud (1967) recognized 2 types of metrocyte—eumetrocytes reproducing by fission ("scissiparity"), and heterometrocytes forming 2 endodyocytes by endodyogeny; however, others do not recognize these types and say simply that reproduction is by endodyogeny. At any rate, the metrocytes divide repeatedly, each time becoming more like banana-shaped merozoites, and are finally recognized as such. The merozoites (bradyzoites) occur in older sarcocysts and eventually replace the metrocytes entirely. They are about 12–15 x 3–4 μm, with 22 subpellicular microtubules, 11 rib-like elements (consisting of rows of granules) on the outer surface, a conoid, up to 11 rhoptries, and about 400 micronemes (Müller, Mehlhorn and Scholtyseck, 1973; Scholtyseck, Mehlhorn and Müller, 1973). They have a single, branched mitochondrion. Mehlhorn et al. (1975) found that the micronemes appear in small vacuoles at the edges of 2 large granular vacuoles in each daughter cell during endodyogeny. Later these vacuoles are divided into numerous vesicular spiral formation centers which produce micronemes at the poles of the young merozoites. Rhoptries originate from densifications within the same large vacuoles which give rise to the micronemes. Thus, the rhoptries and micronemes seem to originate from the same vacuolar substance even though they differentiate into different structures. Porchet-Henneré (1975) said that the micronemes look like rice grains and, contrary to previous statements, are independent of one another. She also said that there are 2 rhoptries and that 2 additional microtubules inside the conoid end abruptly a little behind the conoid. She saw 2 or 3 polar rings and said that the conoid itself consists of about 20 oblique, spirally coiled microtubules.

Porchet and Torpier (1977) studied the merozoites by the freeze-

fracture technique. The outer membrane of the pellicle is continuous and has an apical 8 + 1 particle rosette in the P-fracture face. The inner membrane complex is made of rectangular flattened vesicles aligned in 11 longitudinal rows and joined in a puzzle-like fashion. There is a conical plate opened at the anterior apex by a vertical ridge. The membranes of the inner complex have a parallel alignment of particles in the P faces. Some of these particles are joined and continuous with double rows radiating in the apical cap. These rows correspond in number and arrangement with the underlying microtubules. The membranes of the rhoptries have periodic circular arrays of particles.

Acid phosphatase is present in the endoplasmic reticulum of the metrocytes and merozoites, alkaline phosphatase is present along the outer membrane, and adenosine triphosphatase in the endoplasmic reticulum, in the perinuclear space, between the 2 inner membranes of the 3-layered pellicle, and only slightly in the mitochondrion (Mehlhorn and Scholtyseck, 1973a, 1974b).

Gamogony. This process occurs in the lamina propria of the villi of the cat small intestine; it takes less than a day (Becker, Mehlhorn and Heydorn, 1979).

Prepatent Period. Ten to 14 days (Rommel, Heydorn and Gruber, 1972; Mehlhorn and Scholtyseck, 1974b; Rommel et al., 1974; Sela Perez, 1979).

Patent Period. 4–53 days or more (Rommel, Heydorn and Gruber, 1972; Mehlhorn and Scholtyseck, 1974a; Rommel et al., 1974; Sela Perez, 1979).

Pathogenicity. This species is apparently only slightly if at all pathogenic for either lambs or cats.

Immunity. Immunity is not produced in cats by previous infection. Rommel, Heydorn and Gruber (1972) found that a second infection of cats was followed by a prepatent period of 11–15 days and a patent period of 25–47 days, as compared with 11–12 and 4–53 days, respectively, in cats upon primary infection.

Aryeetey and Piekarski (1976) found that there was no cross-reaction in the indirect immunofluorescence test between *Sarcocystis* and *Toxoplasma.* They also found that freezing or cooking *S. gigantea* sarcocysts destroyed their ability to induce the formation of antibodies in rats fed frozen or cooked mutton.

Cross-Transmission Studies. Ashford (1977) transmitted this species

to the red fox *Vulpes vulpes;* its sporocysts in this host were 13–14 x 9–10 μm. The dog (Rommel, Heydorn and Gruber, 1972) and laboratory rat (Aryeetey and Piekarski, 1976) cannot be infected. Awad (1973) said that he transmitted this species from sheep to sheep by feeding "macrocysts" or feces.

Cultivation. Dubremetz, Porchet-Henneré and Parenty (1975) cultivated *S. gigantea* in embryonic sheep kidney tissue culture, inoculating it with sarcocysts from the sheep esophagus. The crescent-shaped "stage 1" bradyzoites entered the cells and transformed into thicker, oblong forms (called "stage 2") and then into ovoid "stage 3" parasites.

Remarks. Rommel, Heydorn and Gruber (1972) were the first to find that this sheep species has a predator-prey life cycle with asexual stages in the sheep and sexual stages in the cat. Euzéby, Lestra and Gauthey (1972), Vershinin (1973), Munday (1978), and others confirmed their discovery.

Collins and Charleston (1980) found that sarcocysts from the sheep esophagus survived 10 minutes at 52.5 C but not 10 minutes at 60 C or 20 minutes at 55 C; they survived 60 days at –14 C, 20 days at 4 C and 13 days at 10 C. They recommended treatment of sheep meat for 10 minutes at 60 C to make it noninfective for cats.

Sarcocystis gusevi Krylov and Sapozhnikov, 1965

Type Definitive Host. Unknown.

Type Intermediate Host. Argali *Ovis ammon polli.*

Location. Sarcocysts in skeletal muscles of argali.

Merogony. The merozoites are elongate, 11–14 x 5–8 μm (Krylov and Sapozhnikov, 1965). They did not give dimensions for the sarcocysts themselves.

Remarks. Whether this is a valid species is open to question. Its relationship to *S. gigantea* and *S. tenella* should be investigated.

Sarcocystis medusiformis Collins, Atkinson and Charleston, 1979

Type Definitive Host. Domestic cat *Felis catus.*

Type Intermediate Host. Domestic sheep *Ovis aries.*

Location. Sarcocysts in muscles of sheep, but not in esophageal muscles. Oocysts and sporocysts in cat intestine.

Oocyst Structure. Oocysts unknown. Sporocysts 10–13 x 7–9 (mean

12 x 8) μm (not significantly different from those of *S. gigantea).* No other structural information given.

Merogony. Collins, Atkinson and Charleston (1979) said that the sarcocysts are large and thin-walled, without septa. In contrast, those of *S. gigantea* are thick-walled and have septa. The wall of *S. medusiformis* sarcocysts has rounded villi, and blister-like invaginations are found only at its base; snake-like filaments of even width except for their swollen ends arise from the villar and intervillar surfaces and branch occasionally. There is no collagenous secondary wall. They gave no further structural information.

Prepatent Period. 11–20 days.

***Sarcocystis tenella* (Railliet, 1886) Moulé, 1886**

Synonyms. Miescheria tenella Railliet, 1886; *Balbiania gigantea* Railliet, 1886 in part; *Sarcocystis ovicanis* Heydorn, Gestrich, Mehlhorn and Rommel, 1975; *Isospora rivolta* free sporocysts of Gassner (1940), Levine and Ivens (1965) and *auctores* in part; *Isospora bigemina* large form of Mehlhorn, Heydorn and Gestrich (1975) and Heydorn, Mehlhorn and Gestrich (1975) in part; *Endorimospora ovicanis* (Heydorn, Gestrich, Mehlhorn and Rommel, 1975) Tadros and Laarman, 1976; *Hoareosporidium pellerdyi* Pande, Bhatia and Chauhan, 1972 (probably); *Cryptosporidium vulpis* Wetzel, 1938 (probably); *C.* sp. Bearup, 1954 (probably). (Ashford, 1977 considered *Isospora bigemina* to be a synonym of *S. tenella.)*

Type Definitive Host. Domestic dog *Canis familiaris.*

Other Definitive Hosts. Coyote *Canis latrans,* red fox *Vulpes vulpes,* probably dingo *C. dingo.*

Type Intermediate Host. Domestic sheep *Ovis aries.*

Location. Gamonts, gametes, zygotes, oocysts and sporocysts most numerous in subepithelial tissue at tips of villi in proximal third of small intestine of dog (Munday, Barker and Rickard, 1975). Earlier meronts in endothelium of arteries and arterioles of many organs, including brain of sheep. Late meronts (sarcocysts) in striated muscles of sheep.

Oocyst Structure. Spherical before sporulation, but dumbbell-shaped, with a thin wall stretched between the 2 sporocysts after sporulation, without micropyle, residuum or polar granule. Sporocysts ellipsoidal, with one side flatter than the other, 13–16 x 8–11 (mean 14–15 x 9–10) μm, with smooth, colorless to very pale yellow wall

about 0.5 μm thick, without Stieda body, with residuum. Sporozoites banana-shaped, with one end rounded and the other bluntly pointed, about 11 x 2–3 μm, lying lengthwise in the sporocysts, usually with a clear globule near the wide end (Levine and Ivens, 1965; Rommel et al., 1974; Munday and Rickard, 1974; Munday and Courbold, 1974; Munday, Barker and Rickard, 1975; Heydorn et al., 1975). The sporocysts reported by Ashford (1977) from the red fox were 13–14 x 9–10 μm.

Merogony. There are 3 meront generations in sheep. The first generation is small. Munday, Barker and Rickard (1975) found meronts in the endothelium of arteries and arterioles in many organs (but not in the brain) of a lamb 15 days after feeding it sporocysts from the dog. They found smaller meronts in the capillary endothelium of many organs, including the brain, of another lamb 24 days after it had been fed sporocysts from a dog. Gestrich, Schmitt and Heydorn (1974) found meronts and merozoites in touch smears of the liver, kidney, spleen, heart, lung, lymph nodes, muscles, diaphragm, esophagus, tongue muscles and small intestine wall in 2 lambs that had been fed 1.6–2.0 million sporocysts from dog feces and that had died 24–25 days later. Heydorn and Gestrich (1976) found merozoites in the blood and meronts in the kidneys of a lamb that had died 25 days after having been fed 2 million sporocysts from a dog. They found only immature sarcocysts containing metrocytes in the muscles of another lamb which had remained apparently healthy after having been fed 100,000 sporocysts and which had been killed 41 days later. They found mature compartmented sarcocysts containing both metrocytes peripherally and infectious merozoites more centrally. Mehlhorn, Heydorn and Gestrich (1975) studied the structure of the muscle meronts (sarcocysts) in the muscles of sheep killed 41, 63 and 81 days after having been fed sporocysts from the dog. The meronts were always in muscle fibers which were never surrounded by fibrillar layers (i.e., there was no secondary, host-generated meront wall). The meront was limited by a unit membrane which was thickened at many places of its interior by osmiophilic material. They called this complex, which was up to 25 nm thick, the primary cyst wall. In old meronts it was folded regularly to form palisade-like protrusions about 3.5 μm long which contained neither microfibrils nor microtubules. With light microscopy the combined protrusions looked like a radially striated "thick wall." Mehlhorn, Hartley and Heydorn (1976)

extended these observations. Beneath the primary cyst wall is a zone of fine granular ground substance which extends as septa to the interior of the sarcocyst, dividing it into compartments.

O'Donoghue (1978) studied the life cycle of *S. tenella* derived from sporocysts from dogs in SPF lambs. He found 3 (and what was probably an optional 4th) meront generations. First-generation meronts were found 6–19 days after inoculation (DAI) in the arteriole endothelia of most organs and tissues except those of the nervous, endocrine and reproductive systems; when mature 12–19 DAI they averaged 22 x 13 μm and contained 18–28 (mean 24) tachyzoites averaging 1.5 x 0.6 μm. Second-generation meronts were found 21–34 DAI in the endothelial cells of capillaries throughout the body; when mature 25–34 DAI they averaged 15 x 11 μm and contained 18–38 (mean 30) tachyzoites averaging 1.6 x 0.5 μm. A few third-generation meronts (?) were found 36 DAI in hepatic sinusoids and lymph node capillaries but they were not considered a necessary part of the life cycle. They averaged 7 x 5 μm and contained 6–9 (mean 8) merozoites averaging 2.1 x 0.6 μm. Developing sarcocysts were found in the skeletal and cardiac muscles and a few in the brain beginning 41 DAI. At first they contained only metrocytes, which averaged 4 x 2 μm, but later (65–134 DAI) they contained both metrocytes and bradyzoites; the former averaged 4 x 3 μm and the latter 9.5 x 4 μm. At 65–134 days the sarcocysts in the muscle fibers were compartmented and 28–184 x 15–36 (mean 95 x 22.5) μm; about 80% had a radially striated wall 1.5–2.4 (mean 1.8) μm thick and about 20% had a smooth wall 0.3–0.7 (mean 0.6) μm thick.

Speer and Dubey (1981) and Dubey et al. (1982) studied the fine structure of first- and second-generation merogony in lambs. The strain they used originated in the feces of a coyote, but the lambs were infected from experimentally infected dogs. They found first-generation meronts in the cells between the endothelium and the internal elastic membrane of mesenteric arteries in lambs 19–21 days after inoculation. They found second-generation meronts in cells associated with capillaries and arterioles in the kidney glomeruli, convoluted tubules and other organs 16–40 days after inoculation. The tachyzoites developed by endopolygeny. First-generation meronts were 19–29 x 7.5–24 (mean 23 x 17) μm and contained 120–240 tachyzoites 5–7.5 x 1–2 (mean 7 x 2) μm. Second-generation meronts were 8–15 x 7–13.5 (mean 13 x 9) μm and contained 32–80 tachyzoites 6 x 1–2 (mean 6 x 2) μm.

Erber (1982) also studied the life cycle of *S. tenella* in the sheep and dog. He thought without proof that *S. ovicanis* differs from this species.

The sarcocysts of *S. tenella* are always microscopic. Railliet (1886) said that the sarcocysts were 500 x 60–100 μm. Those seen by Boch et al. (1979) were 20–580 x 14–60 μm and had "hairs" 2–4 x 0.6–0.9 (mean 2.9 x 0.8) μm. Those seen by Erber (1982) were 300–600 x 20–50 μm and had hair-like protrusions 6–8 x 0.5 μm from 60 DAI onwards. Dubey et al. (1982) said that they were up to 97 x 10 μm 35 DAI and contained 1–3 metrocytes. The first bradyzoites appeared 52–66 DAI. At 75 DAI the sarcocyst walls were striated and the sarcocysts were infective for coyotes.

Gamogony. There is no merogony in the definitive host. Munday, Barker and Rickard (1975) followed the process of gamogony in dogs killed periodically after having been fed infected mutton. They found macrogametes and microgamonts with peripherally developing microgametes in the proximal third of the small intestine 1 day after inoculation. Becker, Mehlhorn and Heydorn (1979) said that sexual stages are formed rapidly, the process being done in a day, at which time they saw oocysts. Dubey et al. (1982) found gamonts in the villar epithelial cells of the small intestine 8–12 hours after inoculation, and sporulation was complete within 8 days.

Prepatent Period. In the dog, 8–14 days (Rommel et al., 1974; Heydorn et al., 1975; Munday, Barker and Rickard, 1975; Dubey and Streitel, 1976) or 10–36 days (Leek, Fayer and Johnson, 1977); in the red fox, 9–10 days (Ashford, 1977); in the dog and coyote, 8–9 days (Dubey et al., 1982).

Patent Period. More than 9 days in the dog (Dubey and Streitel, 1976); more than 30 days in the red fox (Ashford, 1977).

Pathogenicity. This species is highly pathogenic for lambs. Gestrich, Schmitt and Heydorn (1974) found that two 8-week-old lambs fed 1.6–2.0 million sporocysts from dogs had fever, anemia and inappetence 14 days later and died 24–25 days after feeding. Sections of their organs and tissues looked like those of calves that had died after infection with *S. cruzi* sporocysts from the dog. Gestrich, Heydorn and Baysu (1975) reported the same thing of 3 lambs fed 2 million *S. tenella* sporocysts each, as did Heydorn and Gestrich (1976) of 1 lamb. The last reported that a lamb given 100,000 sporocysts died on day 29. Munday, Barker and Rickard (1975) reported that 2 lambs fed sporocysts died 42 and 104 days later after an illness char-

acterized by anemia and poor condition. They found mature meronts in cells of the brain 42 days after inoculation; they were associated with nonsuppurative meningoencephalitis. They also found developing sarcocysts associated with myositis in the muscles of this lamb. They found mature sarcocysts in the muscles of the lamb that died 104 days after inoculation, and degenerate and mature sarcocysts together with nonsuppurative meningoencephalitis in the brain.

Leek, Fayer and Johnson (1977) observed anemia, inappetence, weight loss, fever, and reduced serum protein in lambs fed sporocysts from dogs. The lambs that had been given 100,000 sporocysts (the smallest number given) died 27–29 days after inoculation, and those that had been given 1 million oocysts died 24–25 days after inoculation. The most apparent gross lesion was hemorrhage of the striated muscles and visceral organs, the heart being the most severely affected.

Munday (1979) found that oral inocula of 5,000 or 10,000 sporulated sporocysts decreased the weight gains and hematocrits of lambs.

O'Donoghue (1978) reported that 9 SPF lambs given 0.25–0.5 million sporulated sporocysts became ill 21–30 days later; 5 of them died or had to be killed 25–36 days after inoculation (DAI), whereas 4 had recovered by 35–43 DAI. The illness was associated with second-generation merogony. Signs always included marked anorexia, weight loss, elevated body temperatures, developing anemia and finally partial recumbence.

Munday (1981) found that an oral inoculum of 60,000 sporocysts produced abortion in ewes and eventually killed them; myositis, myocarditis, and encephalitis were the main findings at necropsy. He found that oral doses of 2,500 to 60,000 sporocysts depressed the blood hematocrit levels of pregnant ewes for 5–9 weeks.

Pande, Bhatia and Chauhan (1972) said that "*Hoareosporidium pellerdyi*" was mildly pathogenic in the dog, causing aggregations of erythrocytes inside the villar cores and suggestions of congestion in the mucosa of the attacked region.

S. tenella is apparently not pathogenic in the fox.

Immunity. Munday and Corbould (1974) found that the complement fixation test for *S. tenella* was positive in 338 of 339 sheep from islands off Tasmania, where cats did not exist and where the only other mammals were dogs and water rats. They found that a lamb fed sporocysts from the dog developed a complement fixation titer of 1:40 at 41 days of age.

Munday (1981) found that previous infection of sheep with *S. gigantea* did not protect them against subsequent challenge with *S. tenella.*

Leguia and Herbert (1979) found that *Sarcocystis* antigens derived from cattle cross-reacted with sheep sera but not with *Toxoplasma gondii.*

Cross-Transmission Studies. S. tenella is not infectious for the cat (Rommel, Heydorn and Gruber, 1972) or the ox (Gestrich, Heydorn and Baysu, 1975). Dubey, Fayer and Seesee (1978) transmitted "*Sarcocystis* sp." (probably *S. tenella)* from the coyote to the sheep and then to the dog. It caused anemia in the sheep. Dubey (1980) transmitted it from the sheep to the coyote. Fischer (1979) could not infect 2 goats with *S. tenella.* Dubey (1980) could not transmit it from the sheep to the goat via the coyote.

Cultivation. Mehlhorn, Becker and Heydorn (1978) and Becker, Mehlhorn, and Heydorn (1979) cultivated this species from sheep sarcocysts in dog kidney but not in human fibroblast, cat lung or pig lung cells; both oocysts and sporocysts developed in the dog kidney cells. Vershinin, Petrenko and Leont'eva (1979) cultivated it in sheep embryo but not chick embryo fibroblast tissue cultures.

Remarks. In their initial study of sheep *Sarcocystis,* Rommel, Heydorn and Gruber (1972) found only *S. gigantea* in sheep, but Ford (1974, 1975) believed that, because of their close association, the dog must be a more common definitive host than the cat in Australia; he discovered *S. tenella* there and worked out its life cycle. Munday and Corbould (1974) also infected the dog. *S. tenella* was subsequently found in Europe and North America, and this life cycle has been confirmed (Gestrich, Schmitt and Heydorn, 1974).

Fayer and Leek (1979) found merozoites of *S. tenella* in the blood of experimentally infected lambs and transmitted the protozoa to clean lambs by blood transfusion.

Perhaps this is the species that Hartley and Blakemore (1974) found associated with severe encephalomyelitis and myelomalacia in 2 young sheep in Australia. The merozoites in its sarcocysts were 5–7 μm long. This is also perhaps the species that Hilgenfeld and Punke (1974) found in the brain of a sheep in Germany.

Sarcocystis sp. Boch, Bierschenck, Erber and Weiland, 1979

Type Definitive Host. Domestic dog *Canis familiaris* (see Erber and Burgkart, 1981).

Type Intermediate Host. Domestic sheep *Ovis aries.*

Location. Striated muscles.

Prevalence. Boch et al. (1969) found *Sarcocystis* by tryptic digestion in 85% of 427 sheep at slaughterhouses in Bavaria, as compared with 33% by the trichinoscope and 3% by macroscopic examination. They isolated sarcocysts from 67%. Of 500 positive animals, 85% had this species. All were positive by the ELISA test to a *S. gigantea* antigen, including the parasitologically negative ones.

Merogony. According to Boch et al. (1979) the sarcocysts of this form were 240–1,000 x 20–100 μm and had "hairs" 5–11 x much less than 0.5 (mean 7 x much less than 0.5) μm; they were different from those of *S. gigantea* and *S. tenella.*

Sarcocystis sp. Ippen et al., 1974

Type Intermediate Host. Argali *Ovis ammon cycloceros.*

Remarks. Ippen et al. (1974) found this species in the muscles of the argali in East Germany.

Sarcocystis sp. Ippen et al., 1974

Type Intermediate Host. Mouflon *Ovis m. musimon.*

Remarks. Ippen et al. (1974), Blažek, Kotrly and Ippen (1976) and Kavai and Sugar (1976) found this form in the muscles of the mouflon in Czechoslovakia, East Germany and Hungary.

Sarcocystis sp. Ippen et al., 1974

Type Intermediate Host. Urial *Ovis musimon orientalis.*

Remarks. Ippen et al. (1974) found this form in the muscles of the urial in East Germany.

Sarcocystis sp. Mahrt and Colwell, 1980

Type Intermediate Host. Rocky Mountain bighorn sheep *Ovis canadensis.*

Remarks. Mahrt and Colwell (1980) found sarcocysts of this form in the muscles of 3 out of 4 *O. canadensis* in Alberta.

***Toxoplasma gondii* (Nicolle and Manceaux, 1908) Nicolle and Manceaux, 1909**

Synonyms. See Levine (1977) or Levine and Ivens (1981) for a list of 18 synonyms.

Type Definitive Host. Domestic cat *Felis catus.*

Other Definitive Hosts. Jaguarundi *Felis yagouaroundi,* ocelot *F. pardalis,* mountain lion *F. concolor,* Asian leopard cat *F. bengalensis,* bobcat *Lynx rufus,* probably cheetah *Acinonyx jubatus* (Miller, Frenkel and Dubey, 1972; Jewell et al., 1972; Marchiondo, Duszynski and Maupin, 1976).

Type Intermediate Host. Gondi *Ctenodactylus gundi.*

Other Intermediate Hosts. Over 200 species of mammals (including felids and sheep) and birds known. The following discussion has to do primarily with sheep. See Levine and Ivens (1981) for a discussion of *T. gondii* in carnivores, and Levine (1973) for a discussion of *T. gondii* in these and other animals.

Location. Meronts and merozoites in many types of cells of intermediate hosts, including neurons, microglia, endothelium, liver parenchyma cells, lung and glandular epithelial cells, cardiac and skeletal muscle cells, fetal membranes, placenta and leukocytes; in acute infections, merozoites may be found free in the blood and peritoneal exudate (Remington, Earle and Yagura, 1970). Oocysts in small intestine epithelial cells of felids.

Oocyst Structure. The oocysts in felid feces are not sporulated when passed. They are spherical at first, but after sporulation are subspherical, 11–14 x 9–11 (mean 12.5 x 11) μm, without micropyle, residuum or polar granule. Sporocysts ellipsoidal, about 8.5 x 6 μm, without Stieda body, with residuum. Sporozoites about 8 x 2 μm.

Merogony. Animals become infected by ingesting sporulated oocysts or infected meat or animals, or congenitally via the placenta. Congenital toxoplasmosis of the newborn resulting from infection of the mother while she is pregnant is probably the most common form in man and perhaps sheep, but it is not nearly so important in cats (Dubey and Hoover, 1977; Dubey, 1977). Mice can be infected congenitally for generation after generation; Beverley (1976), for instance, reported that it had been transmitted congenitally through at least 9 successive generations in Swiss mice. Experimental infections can be established by intravenous, intraperitoneal or any other type of parenteral inoculation or by feeding. Following experimental inoculation the protozoa proliferate for a time at the site of injection and then invade the blood stream and cause a generalized infection. Susceptible tissues all over the body are invaded, and the parasites multiply in them, causing local necrosis. The parasitemia continues

for some time, until antibodies appear in the plasma, after which the parasites disappear from the blood and more slowly from the tissues. They finally remain only in meronts ("cysts"), and only in the most receptive tissues. In general, the spleen, lungs, and liver are cleared of parasites relatively rapidly, the heart somewhat more slowly, and the brain much more slowly. Residual infections may persist for a number of years.

Merozoites are not sexually programmed (Pfefferkorn, Pfefferkorn and Colby 1977).

When the sporulated oocyst is ingested by a susceptible animal, the sporozoites emerge and pass to the parenteral tissues via the blood and lymph; any type of cell may be invaded. Here they multiply by endodyogeny. The stage at which this occurs has been called a pseudocyst, terminal colony, colony, aggregate stage or group stage; the last term is preferable. The merozoites within it are tachyzoites ("fast," i.e., rapidly developing merozoites); they have also been called proliferative forms and endozoites. (We prefer the term tachyzoite because the "endozoites" are not necessarily *in* anything.) They multiply by endodyogeny. The group stage with its tachyzoites is the stage found in the leukocytes in peritoneal exudate, but it also occurs in other parenteral locations such as the liver, lungs and submucosa; this is the stage occurring in acute toxoplasmosis.

There is an indefinite number of tachyzoite generations. Eventually they enter other cells and induce the host cell to form a wall around them, forming the structure generally called a cyst; actually, it is a pseudocyst or meront. Within it a large number of bradyzoites ("slow" zoites, i.e., slowly developing zoites) is formed by endodyogeny. Bradyzoites are also called cystozoites, or cyst forms; however, these terms are misleading because they do not occur in true cysts. The meronts and bradyzoites are much more resistant to trypsin and pepsin than the tachyzoites, and they may remain viable in the tissues for years. This is the stage found commonly in the brain, but it also occurs in other tissues such as muscle; it is the stage found in chronic infections.

The above meront is the end of the life cycle in all animals except felids, so far as is known. Merogony followed by gamogony occurs in the intestinal epithelial cells of felids (see Levine and Ivens, 1981).

The bradyzoites are 5–8 x 1–2 μm and have a 3-membraned com-

plex at the surface, each membrane consisting of 2 electron-dense layers separated by electron-light material. They have an apical complex consisting of 2 polar rings at the anterior end (and a similar ring at the posterior end); a short, truncate, hollow conoid 0.2–0.35 x 0.15–0.35 μm composed of 6–7 microtubules spirally coiled at an angle of 45–50°; 20 to perhaps 30 (according to some, 5–9) cylindrical or club-shaped rhoptries of variable length, 0.02 μm in diameter after leaving the conoid and thickening posteriorly to 0.08–0.2 μm in diameter; about 50 curved, rod-like micronemes anterior to the nucleus; and 22 longitudinal subpellicular microtubules arising from a ring at the level of the conoid and running posteriorly about ⅕–⅔ of the body length. Just in front of the nucleus is the Golgi apparatus. There are 1 or more micropores in the pellicle. The cytoplasm is somewhat vacuolated and contains numerous ribosomes, rough endoplasmic reticulum, and 1 to several mitochondria. The nucleus is usually spherical or ovoid, about 1–2 μm in diameter, and contains a large nucleolus.

Gamogony. The microgamonts in the intestinal epithelial cells of felids produce 12–32 slender, crescentic microgametes about 3 μm long which have 2 flagella plus the rudiments of a third one (Pelster and Piekarski, 1971). The macrogametes simply grow. Fertilization takes place and the resultant zygotes form walls around themselves, become oocysts, and are released into the intestinal lumen.

Prepatent Period. In cats this period is 3–5 days after feeding parenteral meronts, 7–10 days after feeding merozoites and 20–24 days after feeding fecal oocysts (Frenkel, Dubey and Miller, 1970; Dubey, Miller and Frenkel, 1970b), 2–7 days after feeding "cysts" from mice, and 7 days or more after feeding oocysts from cats (Witte and Piekarski, 1970).

Patent Period. One to 2 weeks in cats.

Pathogenicity. The sexual stages of *T. gondii* are apparently not pathogenic for felids. The parenteral stages may or may not cause signs or symptoms. Toxoplasmosis may vary from an inapparent infection to an acutely fatal one. Asymptomatic toxoplasmiasis is the most common type.

In man, a common form of the disease is the congenital type found in newborn infants. It is characterized by encephalitis, rash, jaundice, and hepatomegaly, usually associated with chorioretinitis, hydroceph-

alus and microcephaly; the mortality rate is high (Feldman, 1953; Feldman and Miller, 1956).

Acquired (i.e., noncongenital) human toxoplasmosis has many different manifestations. Siim (1956) divided the disease into 4 main types. The most common is characterized by lymphadenopathy; it may be febrile, nonfebrile, or subclinical. The second type is a typhus-like exanthematous disease. The third type is a cerebrospinal form, generally fatal, but fortunately rare. The fourth type is an ophthalmic form characterized by chronic chorioretinitis (Siim, 1956; Remington, Jacobs and Kaufman, 1960; Levine, 1973).

Toxoplasmosis in domestic animals is similar to the disease in man. It has been reported in the dog, cat, pig, ox, sheep, goat, squirrel, monkey, marmoset and chicken, among other animals. In sheep, Olafson and Monlux (1942) and Wickham and Carne (1950) described cases of nonsuppurative encephalomyelitis with nervous signs. Cole et al. (1954) isolated *Toxoplasma* from a flock of sheep in which several ewes and lambs died of a disease with respiratory and nervous signs. Toxoplasmosis is an important cause of perinatal mortality in sheep in New Zealand (Hartley and Marshall, 1957). Most of the fetuses are 2 to 4 weeks premature, but some are born dead at full term. About half of them have subcutaneous edema, 75% have intestinal hyperemia, and 80% have multiple, small noninflammatory necrotic foci in the anterior cerebrum (Hartley and Kater, 1963, 1964). Placental lesions are confined to the cotyledons. In about half the ewes, most of these are studded with multiple, tiny white flecks or soft, white nodules 1–2 mm in diameter scattered evenly among the fetal villi; these contain clumps of proliferative trophozoites (Hartley and Marshall, 1957; Hartley and Kater, 1963, 1964). Dubey and Schmitz (1981) reported focal necrosis, calcification of the cotyledons, *T. gondii* tachyzoites in the placenta, many *T. gondii* in the fetal myocardium, and mononuclear infiltration of the fetal heart in the outbreak they described in Oregon. Nicolas et al. (1978) reported abortions and neonatal deaths in 2 flocks of sheep in France.

Hartley and Blakemore (1974) found an unidentified apicomplexan resembling *Toxoplasma* associated with severe encephalomyelitis and myelomalacia in the brains of 2 young sheep in Australia. Merogony was occurring; the merozoites were 5–7 x 2–3 μm and had a conoid, 4 or more rhoptries, many micronemes, a posterior pore and about 24 subpellicular microtubules.

Further details have been given by Levine (1973) and Beverley (1974).

Immunity. Animals that have had toxoplasmosis or toxoplasmiasis are immune to reinfection. Various serologic tests have been recommended for diagnosis. Kagan (1980a, 1980b) said that the dye test is probably the best, but that the indirect hemagglutination and indirect immunofluorescence tests are used routinely by most laboratories and that they are very good. He recommended the indirect immunofluorescence test but said that the ELISA and FIAX techniques are just as good.

T. gondii does not cross-react serologically with other coccidia (except *T. bahiensis)* (see Piekarski and Witte, 1971; Aryeetey and Piekarski, 1976).

Cross-Transmission Studies. Many animals are readily susceptible to parenteral infection with *T. gondii.* Advantage has been taken of this fact in diagnosis. The most certain method of diagnosis is by isolation of the parasites themselves; this is done by inoculation of experimental animals. Mice are usually used for this purpose. Eichenwald (1956) considered mice, golden hamsters and guinea pigs the most sensitive animals in his experience. Simitch, Petrovitch, and Bodjochki (1956) preferred the ground squirrel *Spermophilus citellus,* whereas Lainson (1957) recommended the multimammate rat *Rattus coucha.*

Cultivation. T. gondii is readily cultivated in tissue culture and chicken embryos. It was first cultivated in both by Levaditi et al. (1929), and has since been cultivated by many persons.

Remarks. This has been a much abbreviated review of *T. gondii* infections. The literature on this coccidium is vast. Jira and Kozojed (1970) published a 2-volume bibliography with 7,763 entries for the period 1908–1967, and (1983) a 2-volume bibliography for 1968–1975; many more papers have been published since then. Various aspects of the disease have been reviewed since 1972 by Frenkel (1973, 1974, 1974a), Jones (1973), Levine (1973), Siim (1974), Sénaud and Mehlhorn (1975), Beverley (1976), and Overdulve (1978) among others.

The fact that *T. gondii* is a coccidium having an oocyst in cats like that of *Isospora* was discovered independently by Work and Hutchison (1969, 1969a) and Hutchison et al. (1970) in Scotland and Denmark, Overdulve (1970) in the Netherlands, Weiland and Kuhn (1970) in

Germany, Sheffield and Melton (1970) in Maryland, Frenkel, Dubey and Miller (1970) in Kansas and G. D. Wallace (unpubl.) in Hawaii. It has been amply confirmed since then.

***Toxoplasma bahiensis* (de Moura Costa, 1956 emend. Levine, 1978) Levine, 1983**

See under *Bos taurus*.

***Besnoitia besnoiti* (Marotel, 1913) Henry, 1913**

This species has been discussed above under *Bos*. It has been transmitted experimentally to the sheep (see Peteshev, Galuzo and Polomoshnov, 1974) and cultivated in lamb kidney monolayer cell cultures (Bigalke, 1962).

***Cryptosporidium muris* Tyzzer, 1907**

Synonym. Cryptosporidium agni Barker and Carbonell, 1974

Type Host. House mouse *Mus musculus*.

Other Host. Domestic sheep *Ovis aries*.

Location. Small intestine (brush border of villar epithelial cells).

Merogony. According to Barker and Carbonell (1974), who found this species in sheep in Australia, the trophozoites in the brush border of the villar epithelial cells are rounded, 1.5–3.0 μm in diameter, with a small, dark nucleus. They also found trophozoites containing a large nucleus with nucleolus. The meronts are spherical, about 3–4 μm in diameter, and contain up to 7 merozoites in section. The organisms have a characteristic attachment zone.

Gamogony. Barker and Carbonell (1974) saw bodies about 6 μm in diameter with small, refractile, metachromatic granules around their periphery in the brush borders of villar epithelial cells. They interpreted them as macrogametes.

Pathogenicity. Berg, Peterson and Freeman (1978) found *C. muris* associated with bright yellow, watery diarrhea in the small intestine of 2 lambs in North Dakota.

Remarks. Angus et al. (1982) found this form associated with diarrhea in naturally reared lambs in Scotland.

Discussion

This monograph is essentially an expanded and up-to-date revision of our previous monograph (Levine and Ivens, 1970) on coccidia of ruminants. In the present monograph, not only the coccidia of ruminants but those of other Artiodactyla are included. Furthermore, since the previous monograph was written, it has been discovered that *Toxoplasma, Sarcocystis* and *Besnoitia* are heteroxenous coccidia, so they have been added. In addition, many new species of coccidia have been named since our previous monograph. As a result, the present monograph discusses 217 named species of coccidia in Artiodactyla, including 198 in ruminants, as compared with 100 species discussed in our previous monograph.

Of the total of 217 named species, 167 are *Eimeria,* 7 *Isospora,* 1 *Wenyonella,* 36 *Sarcocystis,* 2 *Toxoplasma,* 2 *Besnoitia,* and 1 *Cryptosporidium,* as compared with 95 *Eimeria,* 4 *Isospora* and 1 *Wenyonella* in our previous monograph. While this may seem quite a large number, it is actually only a small percentage of the number of species that must occur in artiodactyls. As a matter of fact, with the possible exception of a few species such as the roe deer and chamois, only the domestic animals have been studied very much. Indeed, it has been realized only recently that the coccidia of the domestic sheep and goat are not the same.

Eimeria has been described from 39% of the 82 genera and 26% of the 205 species in the order (20% of the 5 genera and 11% of the 9 species of Suidae, and 42% of the 74 genera and 28% of the 192 species of ruminants). These figures may be compared with the 15% of 337 genera and 4% of 2,688 species of rodents given for 176 species of *Eimeria* by Levine and Ivens (1965)(which needs revision) and the 25% of 101 genera and 20% of 248 species of carnivores for all species of coccidia given by Levine and Ivens (1981).

Intestinal coccidia have been described from 6 of the 9 families of Artiodactyla, the exceptions being the small families Tayussuidae, Hippopotamidae and Giraffidae. We are accepting as clearly valid, 14 named species in the pig, 6 in camels, 4 in the alpaca, 4 in *Tragulus,* 12 in *Cervus,* 5 in *Odocoileus,* 6 in *Rangifer,* 9 in *Capreolus,* possibly 17 in the water buffalo or carabao, 18 in the ox and zebu, 5 in *Kobus,* 4 in *Gazella,* 6 in *Saiga,* 5 in *Rupicapra,* 23 in *Capra* (of which 4 are shared with *Ovis),* and 23 in *Ovis* (of which 4 are shared with *Capra).*

We have found no structural character of the oocysts that characterizes the Artiodactyla. A micropylar cap is found in most species of sheep and goat coccidia, but this is not a universal characteristic of these hosts, and it is found in some species from other artiodactyls.

So far as we are aware, there has been a total of 184 cross-infection experiments with *Eimeria,* as compared with 156 given by Levine and Ivens (1970). *E. auburnensis, E. ellipsoidalis* and *E. zuernii* have been transmitted from the water buffalo to the ox, *E. ovoidalis* from the water buffalo to the zebu, *E. caprovina* from the domestic goat to the domestic sheep and back to the domestic goat. Other unquestionable attempts at cross-transmission have failed. One may conclude that *Eimeria* usually cannot be transmitted from one artiodactyl host genus to another except between *Bubalus* and *Bos* and, in 1 case at least, between *Ovis* and *Capra. Sarcocystis* is highly host-specific in the intermediate (artiodactyl) host, but can produce oocysts in a number of definitive (carnivore) hosts. In contrast, *Toxoplasma gondii* has been found in some 200 intermediate hosts, but has been found to produce oocysts only in Felidae.

Summary

This monograph summarizes the known information on taxonomy, synonymy, structure, fine structure, life cycle, hosts, location in the host, pathogenicity, cultivation, epidemiology, immunity and cross-transmission studies of the 217 named species of coccidia of the mammalian order Artiodactyla. These include 167 species of *Eimeria,* 7 of *Isospora,* 1 of *Wenyonella,* 36 of *Sarcocystis,* 2 of *Toxoplasma,* 2 of *Besnoitia,* and 1 of *Cryptosporidium.* In addition, similar data are given for those forms for which insufficient information is available to justify assigning them names.

Eimeria, which is the most common genus, has been described from 39% of the 82 host genera and 26% of the 205 host species. The location in the host is known for 32 species of *Eimeria* (20% of those named), at least some endogenous stages are known for 25 (15% of those named), and presumably complete life cycles have been worked out for only 7 species (4% of those named). Comparable percentages for ruminant *Eimeria* species given by Levine and Ivens (1970) were 18%, 16% and 2%.

A total of 184 cross-infection experiments has been carried out with 59 species of *Eimeria* from 17 donor host species. *E. auburnensis, E. ellipsoidalis* and *E. zuernii* have been transmitted from the water buffalo to the ox, *E. ovoidalis* from the water buffalo to the zebu, and *E. caprovina* from the domestic goat to the domestic sheep and back. Other unquestionable attempts have failed. It is concluded that the artiodactyl species of *Eimeria* are highly host-specific, except between *Bubalus* and *Bos* and, in 1 case at least, between *Ovis* and *Capra.*

The following new combinations are proposed: *Eimeria* sp. (Bhatia, 1968) for *E. cheetali* Bhatia, 1968 in *Antilope cervicapra; Sarcocystis* sp. (Pethkar, 1980) for *Sarcocystis moulei* of Pethkar (1980) [*non*] *S. moulei* Neveu-Lemaire, 1912 in *Capra hircus.*

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Plates

Plate 66

Fig. 292. *E. perminuta.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965). X 1,600.

Fig. 293. *E. neodebliecki.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965). X 1,600.

Fig. 294. *I. suis.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965). X 1,600.

Fig. 295. *E. debliecki.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965). X 1,600.

Fig. 296. *E. polita.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965—cited as *E. cerdonis).* X 1,600.

Fig. 297. *E. parahi.* Sporulated oocyst from *Axis porcinus* (from Pande, Bhatia, Chauhan and Garg, 1970). X 1,350.

Fig. 298. *E. guevarai.* Sporulated oocyst from *Sus scrofa* (from Romero and Lizcano, 1971). X 300.

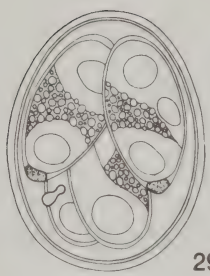
Fig. 299. *E. porci.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965). X 1,600.

Fig. 300. *E. suis.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965). X 1,600.

Fig. 301. *E. spinosa.* Sporulated oocyst from *Sus scrofa* (from Vetterling, 1965). X 1,600.



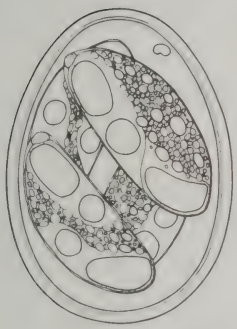
292



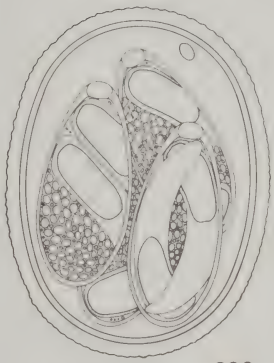
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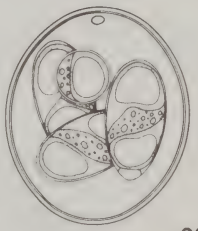
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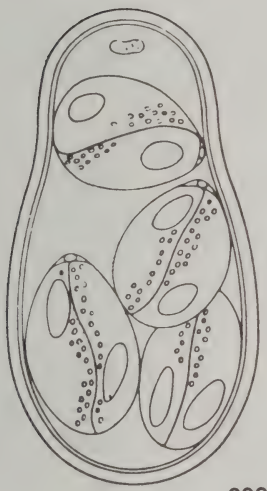
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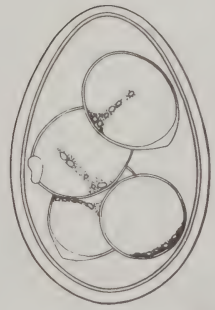
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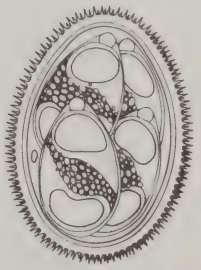
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Fig. 307. Sporulated sporocyst.

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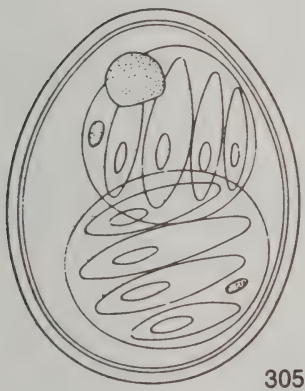
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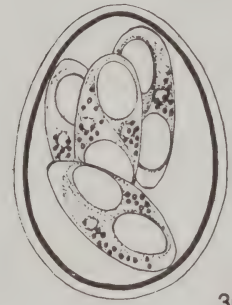
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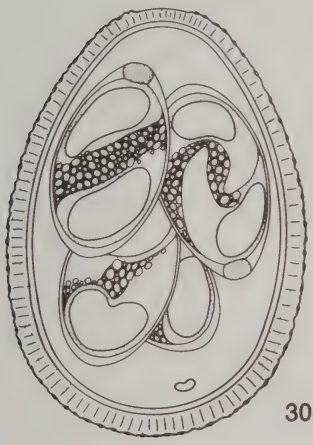
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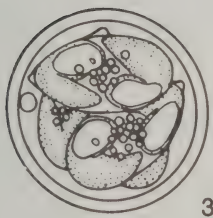
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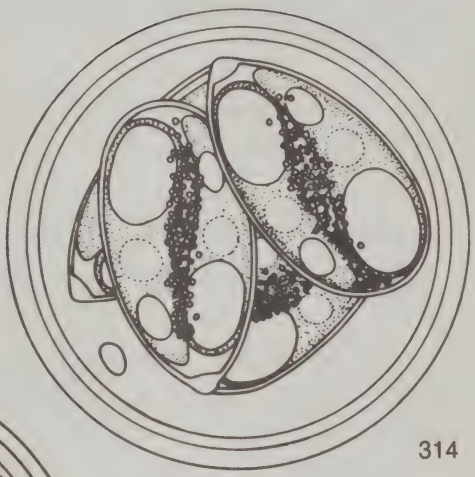
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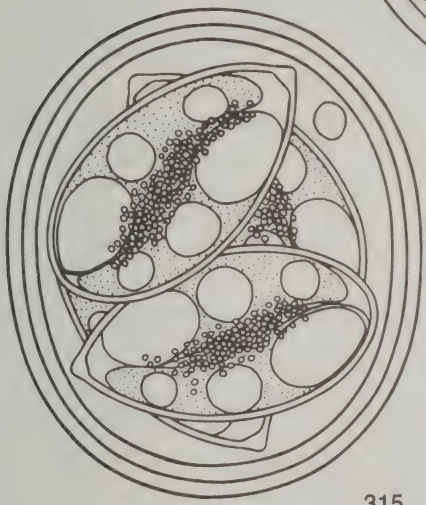
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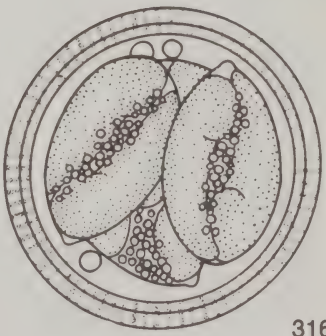
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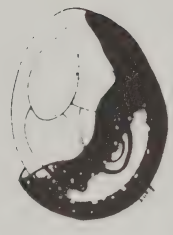
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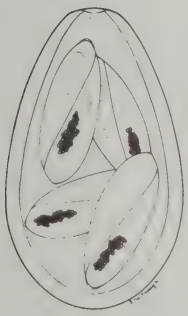
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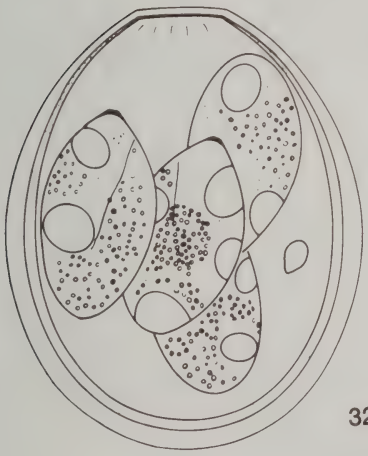
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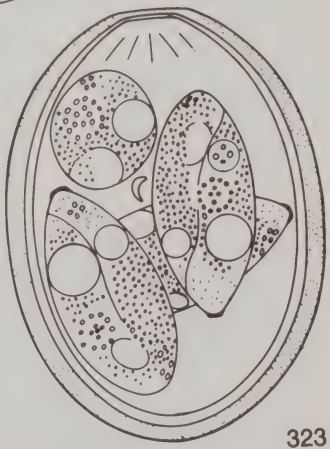
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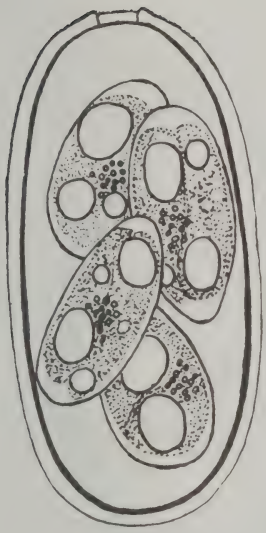
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Fig. 326. Sporulated sporocyst.

Fig. 327. Sporulated oocyst.

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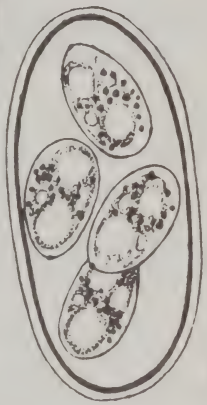
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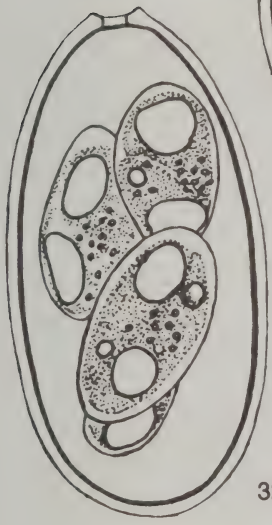
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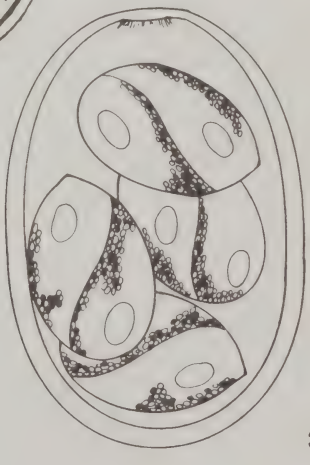
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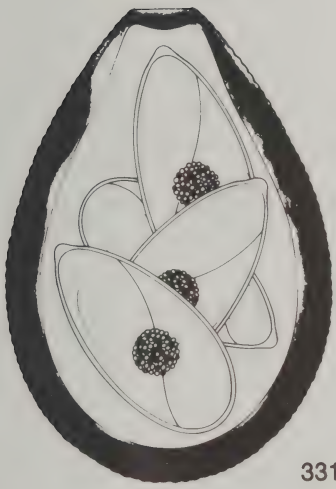
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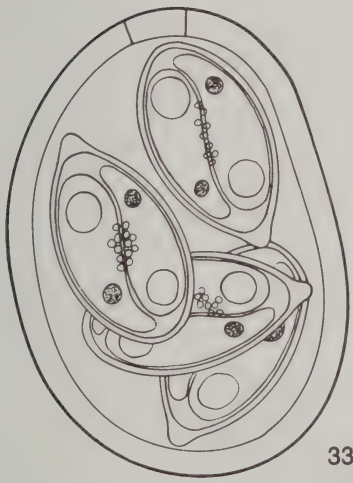
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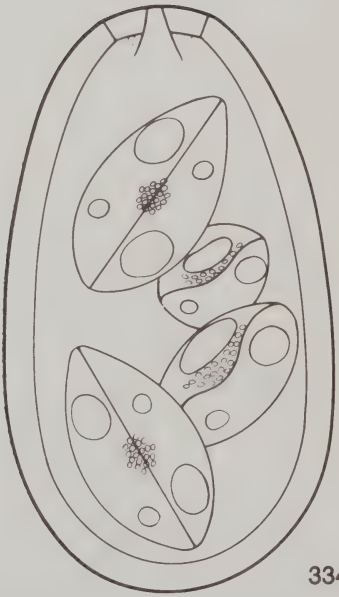
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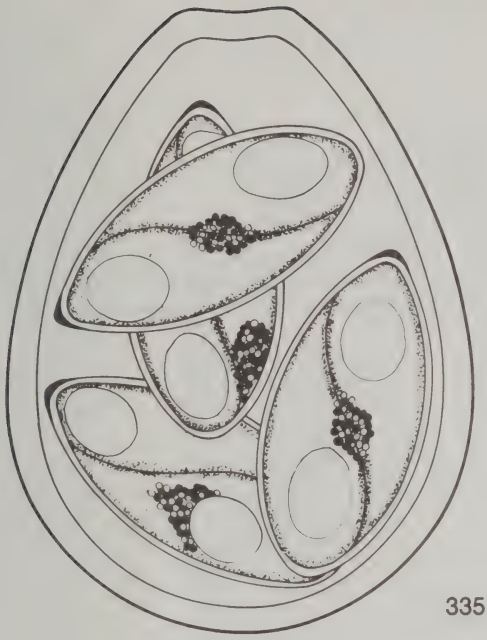


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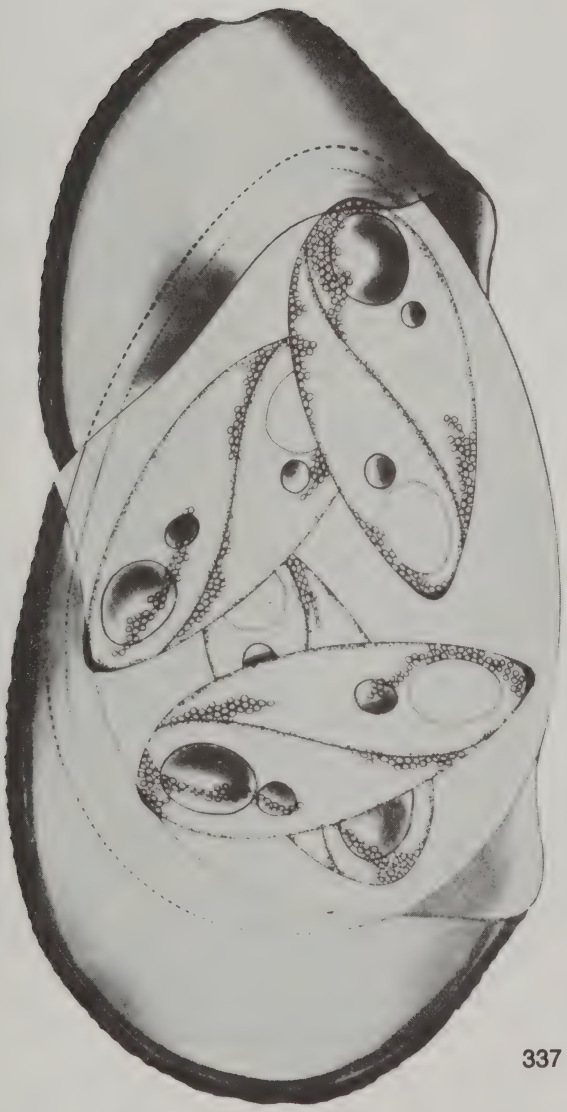
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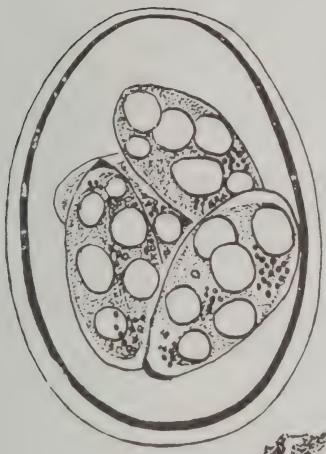
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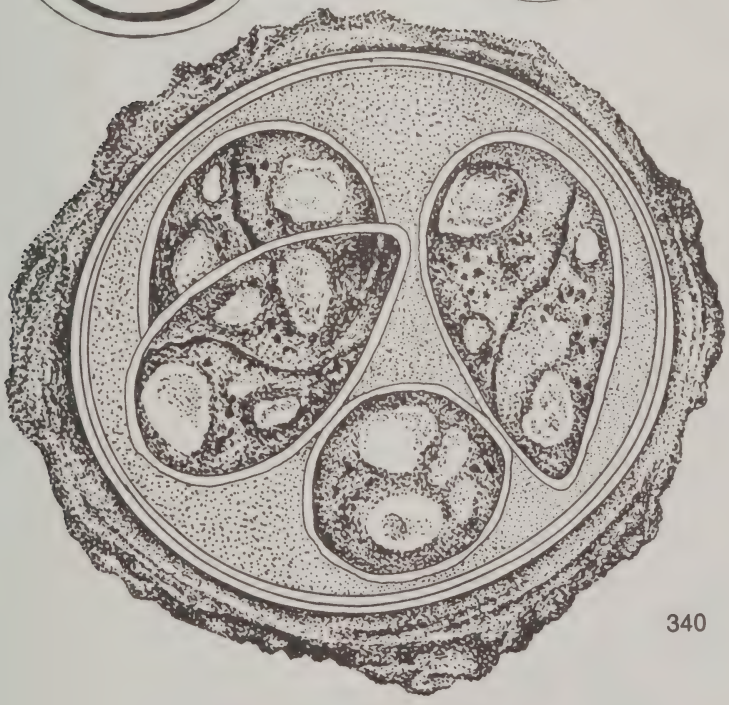
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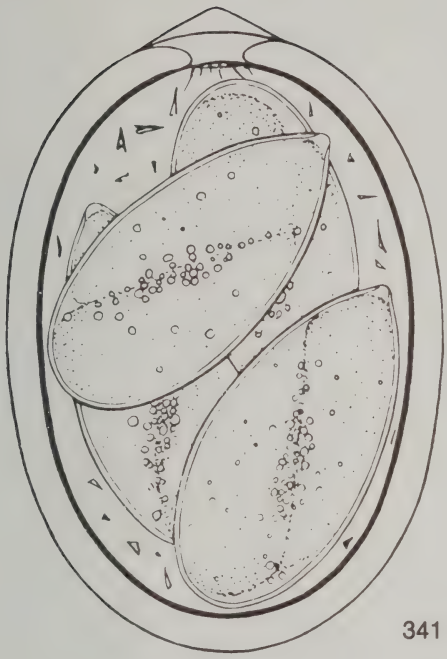


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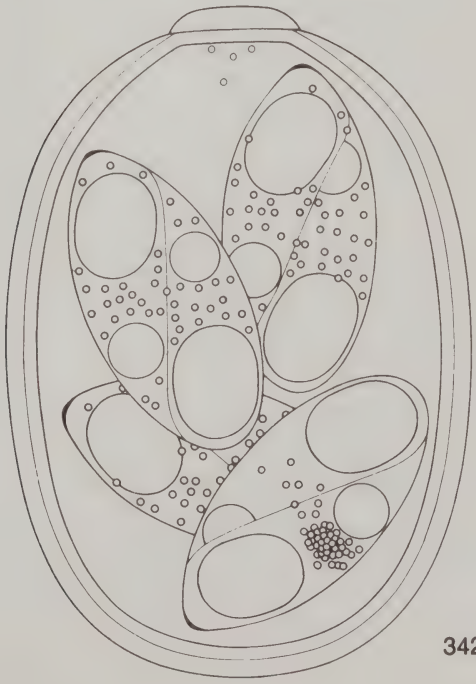
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